GEOGRAPHIC VARIATION IN SLASH PINE (Pinus elliottii Engelm.)

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INTRODUCTION

When a plant species occurs over a wide geographic range, individuals or populations growing in different localities frequently display differences in one or more traits. This phenotypic variation associated with locality (geographic variation) may be due to environmental or genetic factors, or interactions between them.

Environmental differences are a consequence of modifications caused by habitat factors. Genetic variation associated with locality (racial variation), on the other hand, is due to such mechanisms as mutation, natural selection, hybridization, or combinations of these factors. It basically results from the fact that the individuals within populations differ genetically. The genetic heterogeneity between individuals is caused by mutation or hybridization. It is maintained by intricate mechanisms inherent in most species, enhancing chances of survival of the species in a constantly changing environment. This genetic variation among individuals is the basis for racial variation.

If the localities are characterized by different environments, and if some degree of reproductive isolation is present, racial variation will occur. Plants that are genetically most suited to their particular habitat will survive and reproduce in greater numbers than those not so well endowed. Some degree of reproductive isolation is necessary because if interbreeding occurs randomly throughout a species range, natural selection in a given locality would merely result in a change in the mean of the whole species. In forest trees, sufficient isolation is provided by the limited distance of pollen and seed dispersal.

1

Although natural selection is the most important cause of racial variation, it is believed that such variation may also result from chance fluctuations in gene frequencies (genetic drift) leading to fixation of genes. Genetic drift is most apt to occur in small, isolated populations and environmental differences need not be present.

Geographic variation occurs in characteristic patterns, depending upon the nature of the forces that caused it. Since climatic factors are often important natural selection forces, and since climate often changes gradually over a species range, the pattern of racial variation frequently is continuous or climal. However, relatively uniform and discontinuous habitats may cause relatively discrete populations or ecotypes. Likewise, present or past isolation may cause ecotypes or combinations of both climal and ecotypic variation.

Needless to say, geographic variation in forest trees is common, and it is of great interest to forest land managers and forest scientists. The nature of geographic variation (i.e., the proportion of environmental and genetic components) is important to land managers because if differences in economically important traits are genetic they must use care in selecting sources of seed for forest planting. Likewise, forest geneticists are keenly aware of the possibilities of capitalizing on racial variation in development of superior strains. Taxonomists are interested in patterns of variation in their attempts to classify trees on both the species and subspecies level.

The present study was designed mainly to investigate the nature and patterns of geographic and racial variation for a number of characteristics in slash pine (Pinus elliottii Engelm.), one of the

more important commercial trees of the Southeast. Secondary objectives were (1) to search for causes of patterns of variation that might be found, and (2) to compare the magnitude of variation associated with localities against that associated with individuals within localities.

REVIEW OF LITERATURE

General

It is probably safe to say that geographic variation has been studied in all commercially important forest tree species and in many of the noncommercially important ones. Langlet (1938) summarized much of the early work. Several recent publications include brief reviews of much of the past literature: Dorman (1952), Critchfield (1957), Echols (1958), Squillace and Bingham (1958), Callaham (1962), and Langlet (1963).

These studies have demonstrated that racial variation is prevalent in forest trees, although some species such as red pine (P. resinosa Ait.) showed no, or relatively small, variation in some traits (Buckman and Buchman, 1962; and Wright et al., 1963). As might be expected, differences were found to be greatest, or most prevalent, where the species range covered a large geographic area, such as ponderosa pine (P. ponderosa Laws.) and Scotch pine (P. sylvestris L.). However, variation has been found even in trees having a relatively small geographic range, such as sand pine (P. clausa (Chapm.) Vasey) (Little and Dorman, 1952a), and western white pine (P. monticola Dougl.) (Squillace and Bingham, 1958).

Many of the patterns reported contained an element of continuous or clinal variation. Where the variation is a result of gradual changes in climatic or geographic features, and where complete reproductive isolation is absent, one might, of course, expect the variation in plant characteristics to be continuous. Stebbins (1950, p. 44) expressed the opinion that most species with a continuous range, encompassing changes in latitude or climate, will be found to possess clines for physiological characteristics adapting them to conditions prevailing in various parts of their range. Numerous patterns showing continuous variation associated with rainfall have been reported (Larson, 1957; Thorbjornsen, 1961; Goddard and Strickland, 1962; and Squillace and Silen, 1962). Elevational trends were reported by Callaham and Liddicoet (1961) and Critchfield (1957). Numerous instances of gradual changes associated with latitude or length of photoperiod have been found (Langlet, 1936; and Schoenike and Brown, 1963).

One frequently also sees in the literature evidences of ecotypic patterns of variation (for examples, see Wright, 1944; Pauley and Perry, 1954; Vaartaja, 1954; Squillace and Bingham, 1958; and Wells, 1962). However, some of these authors used the term broadly, applying it to patterns which are genetic and adaptive but not necessarily discontinuous. Too, there is often some question as to whether the ecotypic variation occurs exclusive of other types.

Theoretically, distinct ecotypes with no element of continuity can occur in a species having geographical isolation, and in which genetic adaptation to a uniform habitat (such as soil or exposure) has occurred. However, since the habitat within a species range or within parts of a species range often varies continuously, combinations of patterns are more likely. Thus, it is possible to visualize a situation in which a species occurs in geographically isolated groups, with ecotypic variation occurring among groups as a result of adaptation or genetic drift, or both. But with the climate varying continuously through the range we could have clinal variation occurring both within and between the ecotypes. This may indeed be the situation in some species such as ponderosa pine, in which elevational gradients were reported by Callaham and Liddicoet (1961), and in which ecotypes were delineated by Wells (1962). In this same species, Squillace and Silen (1962) pointed out apparent clinal variation associated with climatic variables but acknowledged that likelihood that discontinuities also occurred; irregularities in a clinal pattern were illustrated by Callaham and Hasel (1961). Clausen et al. (1948) found clinal trends for height of plant between climatic races of Achillea lanulosa. In Scotch pine, Wright and Baldwin (1957) and Wright and Bull (1963) delineated broad ecotypes within the species range, while Langlet (1936) pointed out that clinal variation for certain characteristics occur both within and between ecotypes of this species.

The existence or nonexistence of the two kinds of variation often becomes a matter of degree, with interpretation highly subject to the opinions of the investigator and confused by terminology. It is no wonder that considerable discussion and debate have resulted on this problem (Turesson, 1936; Faegri, 1937; Langlet, 1936, 1959, and 1963; Kriebel, 1956; and Callaham, 1962). Until more concrete terminology and guidelines for classification are available (if indeed ever) the wise investigator will describe his pattern of variation as best he can without attempting to classify it categorically (Langlet, 1963).

Another type of variation noted rather frequently in the literature is random variation. Here differences among stands sampled within the species range may be real but exhibit no distinctive geographical trends or patterns such as clines or ecotypes. This type of variation is likely to occur where the species range is discontinuous in the present or had been so at some time in the recent past, as exemplified by the random pattern found in the major portion of the range of European black pine (Pinus nigra Arnold) by Wright and Bull (1962). However, random differences have been found for seed germination in slash pine by Mergen and Hoekstra (1954). Likewise, Thorbjornsen (1961) reported random variation for wing length, seed length, cone length, needle length, and frequency of serrations on needle margins in loblolly pine (P. taeda L.). Both of these species have rather continuous ranges. The cause of random variations in such cases is obscure, although partial reproductive isolation which is believed to be common in most trees may have a bearing (Wright, 1943).

Slash Pine

Slash pine, like many pine species, has suffered a confused nomenclature (Little and Dorman, 1954). Recently, these authors (1952b) subdivided it into two varieties, P. elliottii Engelm. var. elliottii, typical slash pine, and P. elliottii var. densa Little and Dorman, South Florida slash pine, formally publishing a description of the latter.

The ranges of the two varieties, as given by Little and Dorman (1954), are shown in Figure 1. The authors showed the varieties as being allopatric, the boundary between them being indicated by the heavy dashed line in central Florida. At a later date, Langdon (1963) published a revised range of the densa variety, extending it northward a considerable distance as shown by the dotted line in Figure 1. He indicated that trees of both varieties occur in the area of overlap. Slash pine does not extend into the Caribbean Islands.

Features which, according to Little and Dorman (1954), distinguish the two varieties are as follows:

Ver. elliottii: Needles in fascicles of two and three, and normal seedlings with erect, slender, pencillike stems.

Var. densa: Needles in fascicles of two (infrequently three); seedling with grasslike, almost stemless stage with many crowded needles, and thick tap root. The wood of this variety is also heavier and has thicker summerwood than the typical variety.

Mature trees of the two varieties also differ somewhat in general appearance. Variety densa is normally shorter, with its stem often forking into large branches and its crown being generally flat-topped and open, compared to the usually taller and relatively narrow-crowned typical variety. However, according to many foresters, these differences

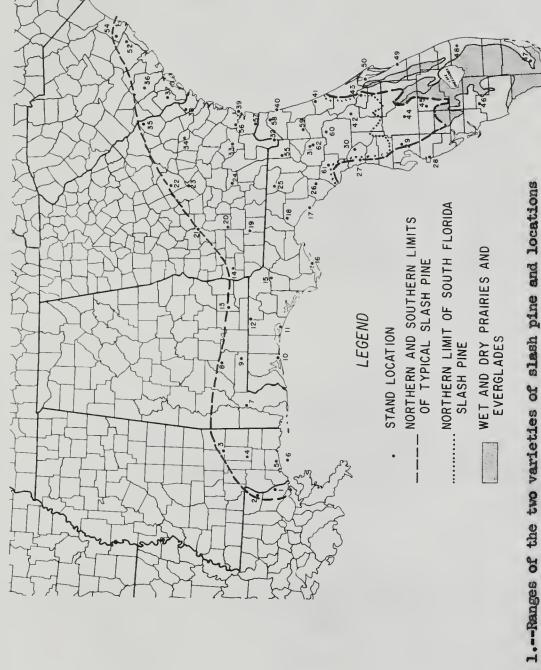


Figure 1 .- Ranges of the two varieties of slash pine and locations of stands sampled.

and even the more distinctive seedling characteristics become obscure in the portions of the species range where the two varieties meet, making it difficult or impossible to separate the two varieties.

Slash pine, being relatively susceptible to fire injury, was originally confined to ponds, pond margins, and other wet areas (Cooper, 1957). With the advent of white man and fire protection it has invaded drier areas, where it grows sympatrically with the relatively fire resistant longleaf pine (P. palustris Mill.).

South Florida slash pine occurs in pure stands on flatwoods sites in the southern part of its range, while to the north it is confined to the wetter sites along streams and in other poorly drained or swampy areas (Langdon, 1963). In the southern portion of its range, there is some degree of geographic isolation between the two coastal areas, caused by the Everglades. The two "prongs" along the coast, however, meet in Polk and Osceola Counties.

A number of seed source studies (studies in which seeds were collected from trees growing in different portions of the species range and planted in a common environment) have been conducted with slash pine. Some of these sampled only the northern portion of the species range (Table 1), while others sampled a relatively broad latitudinal zone (Table 2). The studies were designed mainly to determine variation within the range of elliottii only. However, sampling in some studies of the latter group (Table 2) extended as far south as Polk County, Florida, which is in the area bordering the two varieties (transition zone). In the "Florida-Georgia" experiment (Table 2), a single source well within the range of densa (Collier County, Florida) was included

Table 1. -- Summary of slash pine seed source tests which sampled a relatively narrow latitudinal zone.

Location of test, and authors	Seed sources	: Age of test : (in field)	; Traits showing : significant differences :	: Traits not showing : significant differences
	Number	Years		
Alexandria, La. Derr and Dell (1960) Derr and Enghardt (1960)	2	22		Growth and fusiform rusta
Echols (1960)		73		Stemwood specific gravity and tracheid length
Barrett (1962, 1963a, 1963b)		472		Oleoresin yield, exudation pressure, viscosity, and exudation pressure/viscosity
South Africa (4 localities) Sherry (1947)	₩	6		Height, d.b.h., and tree form, in most localities.
Harrison Exptl. Forest, Miss. Echols (1960)	70	オ		Stemwood specific gravity and tracheid length
N.E. Miss. Exptl. Forest, Miss. Switzer (1959)	9	7	11-year survival, height, d.b.h., and volume	1-3 year survival
Santee Exptl. Forest, S. C. Bethune (1960)	9	12	Height	Survival, d.b.h., and fusiform rusta
Morgan County, Ga. Greene (1962)	70	m		Survival, height, and fusiform rusta

a Gronartium fusiforme (Hedge. and Hunt)

Table 2. -- Summary of slash pine seed source tests which sampled a relatively wide latitudinal zone

Location of test, and authors	sources	(in field)	significant differences	: significant differences
	Number	Years		
"Southwide" (12 localities)	5-6			
Mergen (1954)		N	Height in one locality	
Henry (1959)		10	Fusiform rust ⁸ , in one locality	Fusiform rust ^a , in four localities
Wakeley (1955, 1959, 1961)		rv.	Survival, in 71% of the localities and height in 29% of the localities	Survival in 29% of the localities and height in 71% of the localities
Florida-Georgia (7 localities)	1.5			
Mergen and Hockstra (1954)		(Mursery)	Seed yield and germination	u
Mergen (1958)		(Mursery	Resin ducts, and stonata per mm.	Frequency of serrations on needles and number of rows of stomata
Langdon (1958a)		m	Survival, height, and tip moth damage in one locality	
Squillace and Kraus (1959)		m	Height and survival (aver-ages over all localities)	(v)
Australia (3 localities)	13			
Mikles (1962)		9		Slight differences in growth

a Cronartium fusiforme (Hedge, and Hunt)

b Rhyacionia spp.

along with elliottii sources in one of the seven plantations in the test, but was not included in the statistical tests indicated.

As seen in Tables 1 and 2, significant differences were found more frequently in those studies sampling a broad latitudinal zone than in those sampling only the northern part of the species range. This was especially true for growth rate. In one experiment, latitudinal growth rate differences were mainly due to a sample from Polk County, Florida, in the transition zone and results suggested the existence of natural hybridization between varieties in that area (Mergen, 1954; and Wekeley, 1959). (For further evidences of hybridization see Mergen, 1958.) In still another experiment, growth rate was usually moderately superior among sources from extreme south Georgia and north Florida (north-central region), and it decreased both to the north and south of this area (Squillace and Kraus, 1959). These authors suggested that climatic conditions may be optimum in the north-central region, where superior growth rate may have resulted from relatively strong natural selection for this trait. Resistance to cold damage in the northern fringe and unfavorable distribution of rainfall in the southern areas may have been relatively more important than growth rate in natural selection in these areas.

The results for survival were similar to those for growth rate-differences were found more frequently when a broad latitudinal zone was sampled than when only the northern portion of the species range was sampled. In both the "Southwide" and the "Florida-Georgia" studies early survival was usually greater among northern sources than among southern ones. Some traits, such as stomatal rrequency (Mergen, 1958)

and fusiform rust resistance (Henry, 1959), showed evidences of longitudinal variation in the north.

Several studies other than seed source tests, have also provided information on geographic variation in slash pine. A plantation near Gainesville, Florida, containing clones from phenotypically superior trees selected in various portions of the range of elliottii (Perry and Wang, 1955) showed differences in gum yielding ability at about 7 years of age (Anonymous, 1962, p. 124). A cattle damage test in south Florida, comparing the two varieties of slash pine, showed significant differences in growth and survival (Hilmon, et al., 1962). Stemwood specific gravity and/or summerwood per cent were studied in elliottii trees growing in their natural habitats by several investigators (Larson, 1957; Perry and Wang, 1958; Wheeler and Mitchell, 1959 and 1962; and Goddard and Strickland, 1962). These studies agreed in showing that specific gravity and summerwood per cent increase in going from north to south through Georgia and Florida, and from west to east through the northern portion of the species range. The clinal pattern of variation was shown to be closely associated with seasonal distribution of rainfall, in addition to latitude and longitude. However, the two experiments reported upon by Echols (1960), shown in Table 1, suggest that the pattern in these wood properties is largely environmental rather than genetic. Variation in time of pollen and seed ripening has been reported by Dorman and Barber (1956).

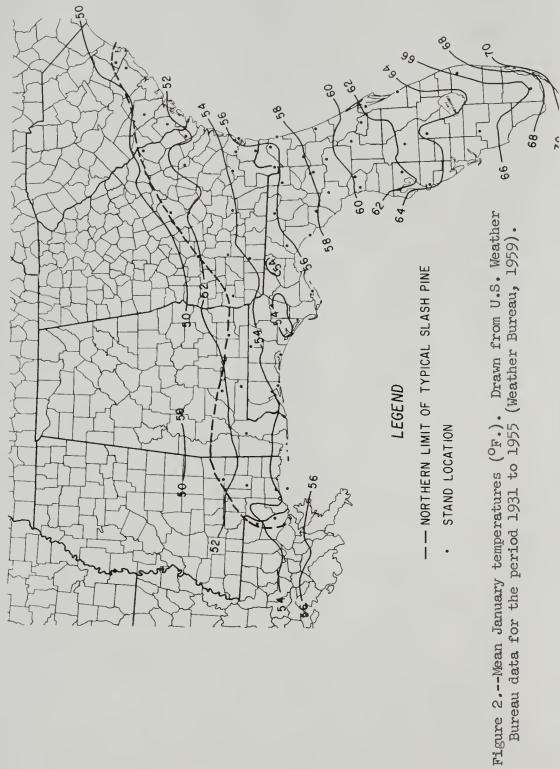
As noted earlier, the above studies dealt mainly with variety elliottii. The possibility of variation within variety dense seems to have escaped study.

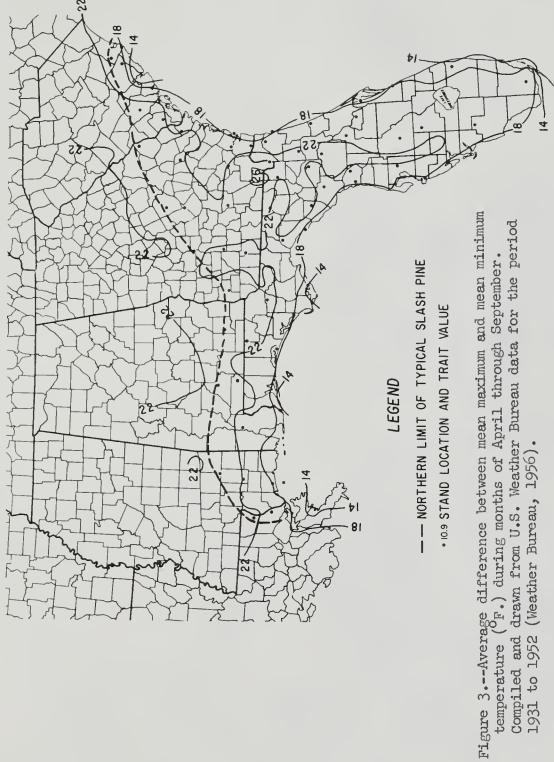
BASIS FOR VARIATION IN SLASH PINE

This section contains an examination of the environmental factors which may have been instrumental in causing geographic and/or racial variation to be reported. Information on climate was freely drawn from U.S. Weather Bureau reports (Weather Bureau, 1956 and 1959).

Climate within the range of slash pine varies from a zone of transition between temperate and subtropical conditions in the north to tropical conditions in the Florida Keys. Temperature variation and other factors are strongly affected by latitude and proximity to the Atlantic Ocean or Culf of Mexico. Summers are relatively long, warm, and humid; winters are relatively mild due to the southerly latitude and warm adjacent sea waters, but periodically cool and cold air from the north invades the region.

Mean January temperatures increase gradually from a low of about 50°F. at the northern extreme in South Carolina to a high of about 70°F. in the Florida Keys (Fig. 2). No such gradient occurs in summer, however, mean July temperatures averaging about 80°-52°F. throughout the region. Length of frost-free season increases from a low of about 240 days at the northern extremes to a high of 365 days in south Florida. The spread between daily maximum and minimum temperature is greatly affected by proximity to the sea, especially during the growing season. For example, the mean spread for the months of April through September varies from as little as 14°F. along the coasts to as high as 26°F. in interior portions of the species range (Fig. 3).





Compiled and drawn from U.S. Weather Bureau data for the period

Mean annual precipitation varies from as high as 64 inches in southeast Florida and southern Louisiana and Mississippi, to as low as 44 inches at the northern limits in east Georgia (Fig. 4). Although the pattern is somewhat erratic there is a general tendency for decreasing rainfall from southern Louisiana, east and northeast to South Carolina, and from south Florida northward.

Seasonal distribution of rainfall shows distinctive patterns.

Precipitation is distributed favorably in the northern portion of the species range, with highs occurring generally in February and March, and July and August. In the south, most of the total rainfall occurs in the midsummer months and wintertime drouths are rather common. The variation expressed in these terms produces continuous patterns. These are well illustrated in maps drawn by Squillace and Kraus (1959) which show patterns of rainfall for January through April, and June through September. The same situation is also expressed in Figure 5 which shows isograms for rainfall from October through May as a per cent of annual. Note that it is low in extreme southwest Florida and increases rather uniformly to the north and northwest.

Estimates of precipitation-evaporation (P-E) ratios were determined for weather stations within the range of slash pine, using the method described by Thornthwaite (1931.) These ratios are measures of precipitation effectiveness and are estimated from mean monthly precipitation and mean monthly temperature, utilizing Thornthwaite's formula or his nomogram. (The latter, a graphical method, was used for the present study). P-E ratios were determined for months of February, March, and April, and summed. These months were chosen because effective rainfall during this period may be more closely

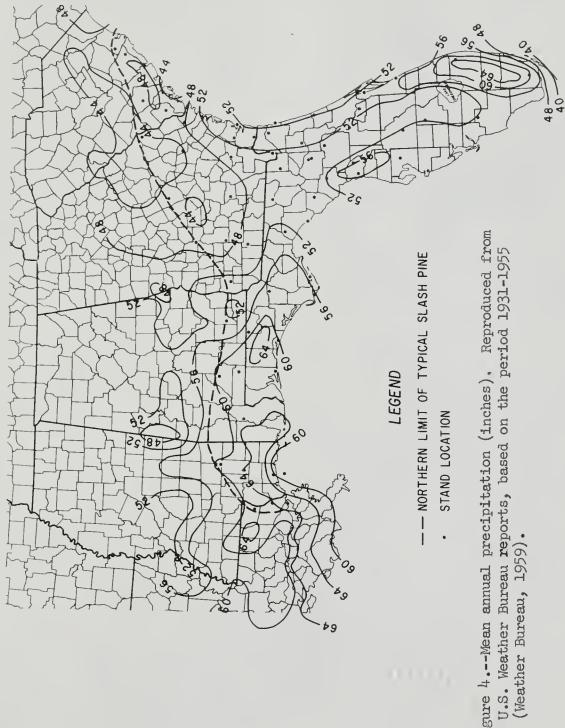


Figure 4.--Mean annual precipitation (inches), Reproduced from

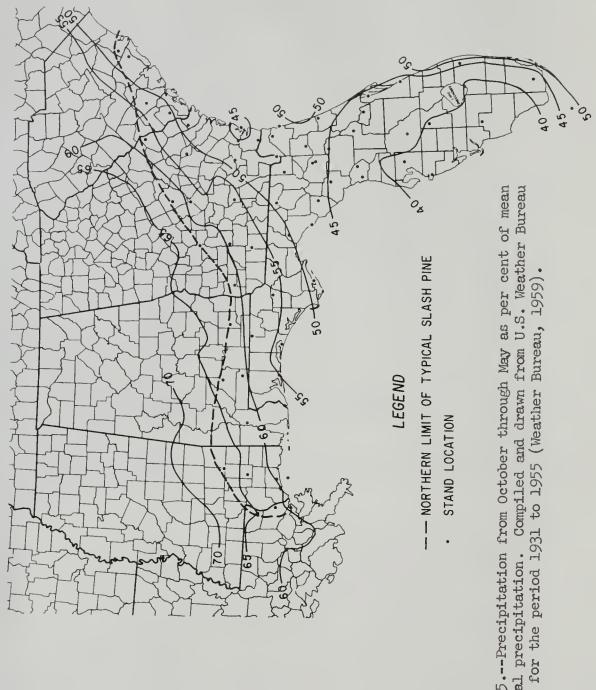


Figure 5.-- Precipitation from October through May as per cent of mean annual precipitation. Compiled and drawn from U.S. Weather Bureau data for the period 1931 to 1955 (Weather Bureau, 1959).

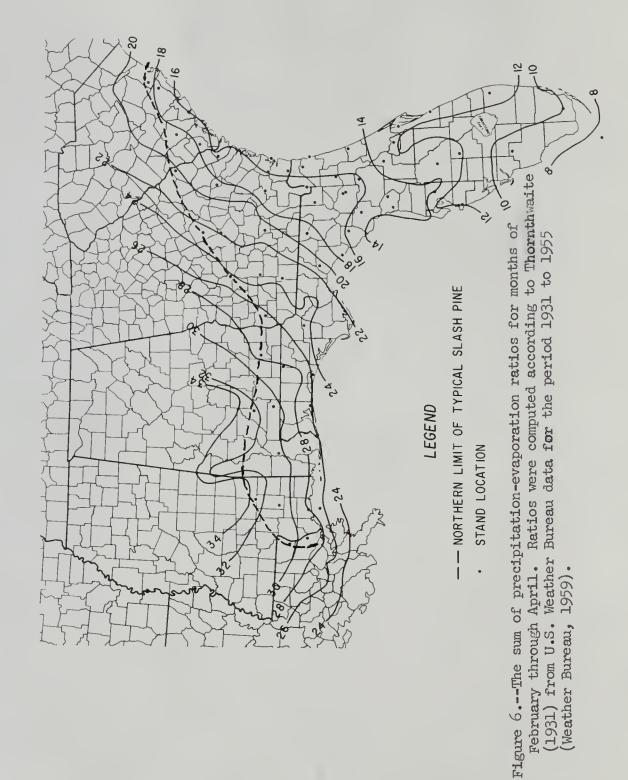
associated with growth of slash pine than rainfall during other periods, as reported by Coile (1936). The data showed a distinctive, continuous pattern (Fig. 6), much like that for October-May precipitation per cent.

Hurricanes are common along the coastal areas (Weather Bureau, 1959). Chances of hurricane force winds are greatest at the southern tip of Florida, and the probabilities generally decrease to the north along the Atlantic coast to southeast Georgia where they increase slightly. On the Gulf coast, probabilities decrease northward to the Tampa region but then become high again in west Florida and south Alabama.

Soils within the range of slash pine are for the most part sandy in texture, and low in mineral nutrients and moisture holding capacity. They are often underlain with hardpans 18 to 24 inches below the surface. Coastal areas are low and flat while the interior portions are generally rolling, with gentle hills and ridges mostly under 200 feet in elevation but reaching as high as 345 feet in Florida, and 600 feet in Georgia. Local variations in soil characteristics, frequently associated with small differences in elevation (as little as several feet), are common. These variations strongly affect tree growth (Cooper, 1957).

Forest geneticists are concerned as to whether or not racial differences associated with local variations in soils are present.

Edaphic races have been reported for some species of plants (Snaydon and Bradshaw, 1961). Most workers feel that this type of variation has not developed in slash pine. Until recently, slash pine occurred only on pond margins. Natural selection probably has not had sufficient time to cause appreciable changes in gene frequencies on the higher areas, especially since these areas frequently are interspersed with flatwoods.



Geological changes during the Pleistocene period (beginning about 3/4 million years ago) undoubtedly had some bearing on the development of variation in slash pine. Following the Kansan glaciation, the Florida peninsula was reduced to a group of small islands extending from Hamilton County in the north to as far as Highlands County in the south (MacNeil, 1950). The second shoreline recognized by MacNeil, following the Illinoian glaciation, shows a similar group of islands but they were larger and the mainland extended as far south as Alachua County. During the mid-Wisconsin glacial recession, much of Florida occurred as part of the mainland, the peninsula extending as far south as Glades County, with a number of islands mostly along the east and southwest coasts. The final and most recent shoreline recognized by MacNeil was of post-Wisconsin origin. Although the degree of inundation was relatively small at this time, a number of islands occurred along coastal regions.

PROCEDURE

Parental Material

The conventional seed source technique was used for this study but with the additional features of: (1) sampling parental materials to measure geographic variation, and (2) maintaining individual mother tree identity in order to study mother tree variation within stands.

In the fall of 1960, mature cones and foliage samples were collected from each of five (in a few instances less) mother trees at each of 55 stands scattered throughout the range of slash pine. Proposed stand locations were predesignated mainly by gridding the area on a map, with a spacing interval of about 50 miles. However, irregularity of the species range, non-forested areas, and other considerations necessitated moving many of the proposed locations so that the actual distribution of the stands only faintly resembles a grid (Fig. 1).

It should be noted that systematic sampling of stands leads to a bias in variance and the magnitude of this bias is unknown. An alternative procedure would have been to sample stands completely at random or to stratify and sample randomly within strata. Systematic sampling was chosen because of a strong desire to include the extremities of the range, and because it was felt that this method would be most suitable for elucidating patterns of variation.

Materials were collected through the aid of cooperators. Instructions included selection of accessible, natural stands as near as feasible to the predesignated points, with the requirements that they (1) be at least 400 feet away from flowering slash pine plantations, (2) be of fruiting age, and (3) not be selected for any particular traits.

Within each stand, mother trees were selected randomly but with restrictions that (1) they be dominants or codominants, possessing mature cones, (2) they be at least 200 but not more than 1,300 feet apart, and (3) they have one or more neighbors within 100 feet. In those areas where the two varieties meet or overlap (transition zone), no attempt was made to select one or the other variety, because (1) identification of the varieties in the mature stage is difficult, as noted earlier, and (2) it was felt that attempted selection would prevent the possibility of determining the population structure of the transition zone. Mother trees within stands were designated "A" through "E". These letters, combined with stand numbers (1 through 55), served to identify all mother trees.

From each tree, 10 to 15 comes and 5 branch shoots were collected from the upper and outer portions of the crowns. Most of the materials were obtained by shooting them out of the trees with a rifle. Plant materials were sent to Olustee, Florida, for processing.

Collections were highly successful but, upon receipt of the materials, the sample from stand 51 was found to be loblolly pine rather than slash pine (identification was verified upon sowing of seed). Hence, this stand was discarded. Also, materials for three mother trees (29E, 48A, and 48C) were missing. Finally, it was later determined that mother tree 21D was apparently a hybrid (or backcross) between slash and longleaf pines, and hence data from this tree were eliminated from analyses. These circumstances reduced the number of stands to 54, and mother trees to 266.

In the late fall of 1960, after cone collection, seven additional stands were designated (numbers 56 through 62) and used for collection of foliage samples (see Fig. 1 for location of these). These supplementary samples were taken mainly to check on what appeared to be unusual results from the main samples and to increase sampling intensity in north Florida. Data from the supplemental samples were not used in statistical analyses but were included with data from main samples in elucidating patterns of variation.

Upon receipt, the unopened cones were counted and 10 (or less when a shortage occurred) were selected from each mother tree and photographed. The negatives were then projected on a microfilm reader and the lengths and diameters (across broadest portion) of each cone were measured. Cones were dried in the open air; then the seeds were extracted and winnowed with a seed blower which removed practically all empty seed. Full seed were then counted, weighed, and stored in a refrigerator at approximately 40°F. until planted.

Branch shoots were handled as follows: Eight fascicles were taken randomly from the central portion of the first flush of the 1960 increment of each branch shoot (40 fascicles per mother tree). The number of needles per fascicle was determined on each of these. Then 3 fascicles were selected randomly from each group of 8 samples (15 per mother tree), and on these the lengths of fascicles and the lengths of the fascicle sheaths were measured. Finally, 2 additional needles were selected from each shoot, again from the central portion of the first 1960 flush of growth (10 per mother tree) and the uppermost 2 inches of each was cut and preserved in formalin-aceto-ethyl alcohol fluid.

The preserved needle specimens were then used for additional measurements as follows: The lower 1/8-inch of each section was cut and examined under a binocular dissecting microscope (45X) and the following measurements taken: (1) Width of the needle, measured across the flat surface or surfaces (binate needles had one flat surface while ternate needles had two), using an eyepiece micrometer; (2) the number of rows of stomata on the flat surface or surfaces; and (3) the number of stomata in two rows, each 1.68 millimeters long (the length of the micrometer scale): for binate needles the second row nearest each edge of the single flat surface was used, while for ternate needles the second row nearest the rounded surface was taken from each of the two flat surfaces. The number of rows of stomata was divided by the total flat surface width in millimeters to obtain "number of rows per millimeter of width." The number of rows per mm. of width was then multiplied by number of stomata per mm. of row to obtain number of stomata per square mm. of needle surface.

Freehand cross sections were then cut from the lower end of each of five needle segments (one per shoot) and mounted in water on microscopic slides. These were then examined under a microscope (100X) and the number of resin ducts and number of layers of hypodermal cells determined. The latter measurement proved difficult. Invariably there was a well defined, thin-walled, outer layer of cells. Inside of it occurred one or more "layers" of thick-walled cells, but these were not always in true layers, the innermost frequently containing sporadic, single cells. However, four points were systematically predesignated on each section (always between stomata) and the number of "layers" counted at each, to obtain an average for the needle.

Progeny Material

Seeds were sown on March 14-15, 1961, in a nursery at Olustee, Florida, in two nursery tests. Nursery Test 1 was designed to obtain maximum development of foliage, and for this reason seeds were sown in plastic pots 6 inches in diameter and 6 inches deep. The design was a randomized block type, with individual tree plots and five replications. From one to three seeds were sown per pot, depending upon the number available, and the seedlings were thinned to one per pot soon after germination.

Nursery Test 2 was designed mainly to produce seedlings in quantity for outplanting, which is not encompassed in this report. However, the material provided an opportunity to obtain more reliable data on seed germination and cotyledon number than could be obtained from Nursery Test 1 and hence was used for this purpose.

In Nursery Test 2, seeds of each mother tree were sown in row plots of 44 seeds each, with 3 replications. But in order to minimize competition effects, the five mother trees of each stand were randomized within stand plots, and stand plots were randomized within replications. Seeds were sown at a spacing of 1 inch within rows and rows were spaced 6 inches apart.

Germination was counted in Nursery Test 2 on March 29, 1961, and again on April 10, 1961. The first count divided by the second count, x 100, gave an index of the speed or rate of germination in per cent, while the latter count (expressed in per cent of seeds sown) alone was used as a measure of germinability. Also, cotyledon counts were obtained on up to 10 randomly chosen seedlings per row in April, 1961.

Total heights and stem diameter outside bark at ground line were measured on the seedlings of Nursery Test 1 on November 3, 1961.

In the late fall of 1961, foliar samples and measurements were obtained from the potted seedlings of Nursery Test 1 as follows: First, counts of the number of needles per fascicle were obtained on each of 10 fascicles taken from each seedling. Fascicles were chosen randomly from the upper portion of the first flush of growth. The foliar material was then handled in a manner similar to that from the parents. However, here fascicle length and fascicle sheath lengths were measured on three fascicles obtained from each seedling and the stomatal, resin duct, and hypoderm measurements were obtained for two needles per seedling.

Analyses

Single variate analyses

Statistical analyses consisted mostly of two types, single variate and multivariate. In the single variate analyses the stands were divided into three groups as follows:

- Group 1. Stands within the range of the elliottii variety, excluding those close to the limits of the densa variety, as follows: Numbers 1 through 26, 31 through 40, 52, 54, and 55. Total, 39.
- Group 2. Stands arbitrarily considered to be within the transition zone between the two varieties: Numbers 29, 30, 41, 42, 44, and 45. Total, 6.
- Group 3. Stands within the range of South Florida slash pine as delineated by Little and Dorman (1954): Numbers 27, 28, 43, 46 through 50, and 53. Total, 9.

Note that the assignment of borderline stands in the transition zone appears inconsistent in some instances, according to limits of the varietal ranges shown in Figure 1. The reason for this is that the assignment of stands into groups was made according to the small-scale map in Little and Dorman (1954), the most recent available range map at the time. The northern limits of var. densa shown in Figure 1 were reproduced from Langdon's (1963) more recent and detailed map, revealing what appears to be inconsistencies.

The purpose of grouping the stands was to provide a means for determining the presence or absence of significant stand differences within varieties. To this extent, limitations imposed by the arbitrary nature of the grouping should be recognized.

The analyses of variance for data from parent tree samples were as follows:

Source of Variation	D.F.	Expected Mean Squares
Groups of stands (G)	2	$\sigma_{M}^{2} + k_{12} \sigma_{S}^{2} + k_{11} \sigma_{G}^{2}$
Stands within groups (S)	51	$\sigma_{M}^{2} + k_{22} \sigma_{S}^{2}$
Mother trees within stands (M)	209	$\sigma_{\overline{M}}^2$
Total	262	

In the above analyses the deficiency in degrees of freedom for mother trees was due to seven "missing" trees (9D, 21D, 29E, 36B, 48A, 48B, and 48C). Tree 2LD was dropped because of evidence that it was a hybrid, while the remaining missing trees were due to lack of samples.

Coefficients for the variance components for all analyses of variance were computed using the technique outlined by Gates and Shiue (1962). For the parent tree analyses the coefficients were as follows:

The analyses of variance for progeny data of Nursery Test 1 were as follows:

Source of Variation	D.F.	Expected Mean Squares
Replications (R)	4	
Groups of stands (G)	2	$\sigma_{\rm E}^2 + k_{13} \sigma_{\rm M}^2 + k_{12} \sigma_{\rm S}^2 + k_{11} \sigma_{\rm G}^2$
Stands within groups (S)	51	$\sigma_{\rm E}^2 + k_{23} \sigma_{\rm M}^2 + k_{22} \sigma_{\rm S}^2$
Mother trees within stands (M)	209	$\sigma_{\mathbf{E}}^2 + \mathbf{k}_{33} \ \sigma_{\mathbf{M}}^2$
Error (E)	1043	OE
Total	1309	

In the above analyses the deficiencies in degrees of freedom for mother trees and error were due to seven "missing" mother trees (21D, 22E, 29E, 42B, 42D, 48A, and 48C) and five "missing" seedlings (7A-4, 9C-4, 38D-1, 46C-4, and 46D-4). Mother tree 21D was dropped for reasons noted earlier, while the remaining missing items were due to lack of samples.

Coefficients computed for the components of variance estimates, were as follows:

$$k_{13} = 4.982$$
 $k_{12} = 23.746$ $k_{11} = 277.504$ $k_{23} = 4.984$ $k_{22} = 24.278$ $k_{33} = 4.980$

The analyses of variance for progeny data of Nursery Test 2 were as follows:

Source of Variation	D.F.	Expected Mean Squares
Replications (R)	2	
Groups of stands (G)	2	$\sigma_{E_1}^2 + k_{12} \sigma_{S}^2 + k_{11} \sigma_{G}^2$
Stands within groups (S)	51	$\sigma_{\mathbf{E}_1}^2 + \mathbf{k}_{22} \sigma_{\mathbf{S}}^2$
Error 1 (E ₁)	106	$\sigma_{\mathbf{E_1}}^2$
Mother trees within stands (M)	202	$\sigma_{E_2}^2 + k_{33} \sigma_{M}^2$
Error 2 (E ₂)	404	o ² / _{E2}
Total	767	

In the above analyses the deficiency in degrees of freedom for mother trees was due to 14 "missing" mother trees (17D, 21D, 22E, 25D, 29A, 29C, 29E, 33C, 41B, 48A, 48B, 48C, 53A, and 53C). Mother tree 21D was dropped for reasons noted earlier while the remaining trees were dropped because of lack of samples.

Coefficients computed for the components of variance estimates for progeny data of Nursery Test 2 were as follows:

$$k_{12} = 14.061$$
 $k_{11} = 159.140$ $k_{22} = 14.223$

$$k_{33} = 3.000$$

The main purpose of the analyses of variance was to obtain objective estimates of the degree of variation associated with the factors studied. To aid in doing this, estimates of components of variance were obtained using the mean squares computed in the analyses of variance and the "expected mean squares" shown above (Snedecor, 1956, p. 261). The estimated components obtained in this manner were finally expressed in per cent of the total of all components (excluding the "replication" component in progeny data).

The component of variance associated with groups was considered to be expressive of the division of the species into the two varieties and the transition zone. That associated with stands within groups expresses the degree of geographic variation within varieties. These two components taken together are expressive of geographic variation for the species as a whole. If either or both of these components were statistically significant and appreciable in magnitude, isograms were drawn in an attempt to elucidate the pattern of geographic variation for the trait concerned.

Note that the above analyses assume homogeneous variances. As will later be seen, variation was frequently found to be greater in some portions of the species range than in others. This circumstance affects the validity of the estimates of variance components and the significance tests. Hence, the estimates and tests should be considered as approximations.

Multivariate analysis

Multivariate analysis was employed to examine the pattern of geographic variation considering a group of traits simultaneously.

Mahalanobis' "generalized distance function" was chosen. (For discussions of this and other multivariate techniques see Rao, 1952; Howell, 1960; Wells, 1962; Wright and Bull, 1962; and Namkoong, 1963.)

This function, D², expresses the degree of relationship between two populations, considering simultaneously the group of traits chosen.

The formula for two traits (X₁ and X₂ is as follows:

$$D^{2} = (\overline{x}_{11} - \overline{x}_{12})^{2} + (\overline{x}_{11} - \overline{x}_{12}) (\overline{x}_{21} - \overline{x}_{22}) + (\overline{x}_{21} - \overline{x}_{22})^{2}$$

$$S_{12}$$

$$S_{2}$$

in which \overline{X}_{11} and \overline{X}_{12} are the means of trait 1 for the first and second populations, respectively; \overline{X}_{21} and \overline{X}_{22} the means of trait 2 for the same two populations; S_1^2 and S_2^2 the pooled estimates of the variances of traits 1 and 2; and S_{12} the covariance of traits 1 and 2.

As can be seen, the magnitude of D² for any two populations increases with increasing difference in the means for each trait, and decreases with increasing variance and covariance within populations.

For more than two traits the formula is more conveniently expressed as follows: $D^2 = \sum_{i=1}^{n} \sum_{j=1}^{n} d_j d_j$

where d_i = the mean population difference for trait i

and d_j = the mean population difference for the jth variable

and S_{ij} = the element in the inverse of the covariance matrix

corresponding to the ith and jth variable.

Using procedures outlined by Rao (1952, pp. 345 and 357), D^2 values were computed for 17 traits, including 4 from the parent tree data (cone length, cone diameter, seeds per cone, and seed weight), and 13 from progeny data (total height, stem diameter, number of ternate fascicles, needle length, sheath length, rows of stomata, stomata per mm., stomata per sq. mm., resin ducts, hypoderm thickness, germinability, speed of germination, and cotyledon number). Since there were 54 stands or "populations" a total of (54) (53) = 1,431 values of D^2 had to be computed. The work was done with an IEM 709 electronic computer at the University of Florida Computing Center.

RESULTS AND DISCUSSION

Results of the single variate analyses and patterns of variation for individual traits will be presented first. Following will be a recapitulation of the individual trait patterns along with a discussion of possible causes of variation. Next will be an analysis of the degree of variation (diversity) among individuals within stands and among stands within varieties and their implications. Then follows the results of the multivariate analysis, and finally a discussion of taxonomic considerations.

Single Variate Analyses

Cone dimensions

Mother tree means of come length varied from 7.0 to 15.5 cm.

(Table 3). Most of the variation was associated with mother trees within stands but stands within groups accounted for a considerable proportion (22 per cent) of it (Table 4). Since little of the variation was associated with groups of stands (6 per cent) the trait was not distinctive for varieties. The stand-to-stand variation exhibited a fairly distinctive pattern, however. Cones were relatively short in southeast Florida and increased to the north (Fig. 7). An east-west maximum occurred near the Georgia-Florida boundary (Walton County, Florida, to Duval County, Florida), above which cone length decreased slightly.

Variance components for cone diameter were rather similar to those for cone length, with stands accounting for a sizable proportion (37 per cent) and with groupings of stands accounting for none of it. Although the variation among stands was not associated with varieties, a fluctuating clinal pattern was apparent (Fig. 8). Cones were thickest

Table 3. -- Means and ranges of variation for parental data

r. R.	ri l	ଷ୍ଟ୍ର ଅଧାର	000	41.0
Hypo- derm layers	Number	2.08 2.13 2.29 2.12	1.5-3.0	1.9-2.4
	Number	6.90	2-13 3-10 3-12	3.0-10.2 4.2-9.4 4.4-9.4
Stomata: Resin per sq.: ducts	Mmber	69.1. 67.6 67.4 68.7	111	53-9± 3 55-81 47-76
Stomata per mm. of length	Number	10.3	7.1-14.0 8.3-12.8 7.4-13.1	8.3-12.4 9.3-12.3 8.7-11.9
Rows of stomata : per mm.	Munber	6.61	FASCICLES 4.2-9.6 4.3-8.5 4.2-8.7	5.3-8.5 5.1-7.5 h.8-7.6
Sheath length	ē	1.83	EDLES, OR 0.9-2.5 0.9-2.7	
Needle: Sheath length: length	Cm.	व्यक्त	NES, NEE 12-30 16-30 15-34	15-27 19-28 18-31
Medles t.per fascicle	Manber	4 2 6 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	AMONG CONUCS, NEEDLES, OR 2-3 12-30 0.9-2.5 2-3 15-34 0.9-2.7	RAMGES ANONG MOTHER TREE 2.0-3.0 15-27 1.2-2.3 2.0-2.4 18-31 1.1-2.3
검	8	331.1	RANGES	17-48 19-40 10-51
Seed	Number	57.2 35.9 34.5 51.2	111	6-127 3-88 1-80
Cone diem-		### # 60 ## #	2.8-5.8 2.8-5.6 2.5-5.3	3.1-5.3
Group Cone	3	10.5	6.8-18.0 6.4-14.0 6.4-16.0	8.2-15.5 7.1-12.3 7.0-15.1
Group		1 2 3 All groups	iαω	400

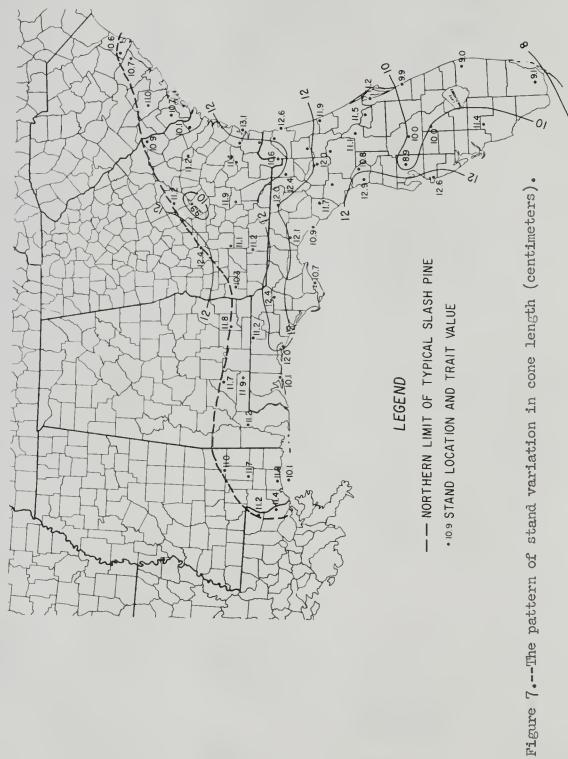
Table 4.--Mean squares and estimates of variance components obtained from analyses of variance of parent tree data

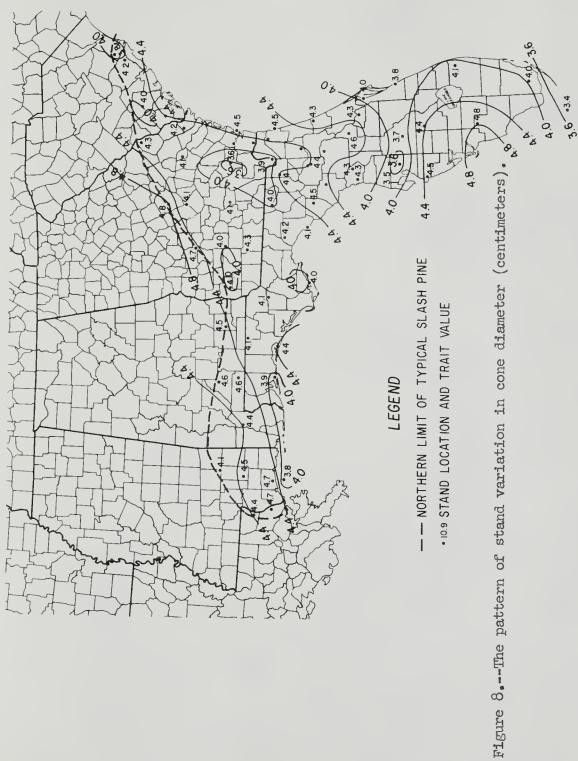
variation	length	:Cone : Cone : Seeds: :length: diam-: per : : eter : cone	Seeds:	Seed : Nees weight: per	Needles : restrictes	Needle:	Needle:Sheath:stomata length:length:per mm.	stomata : per mm :per mm. : of of width:length	per mm. of length	Stomata per	Resin	Hypo-derm
					MEAN	SQUARES						
Groups 13.8 .50 Stands/G 4.8** .50** Mother trees/S 1.913	13.8		1270** 180** 41	114 98** 33	**60.0	143.4**	.013 .135**	3.58**	3.12**	888	3.15	.80** .04**
			ESTIM	MATED CO	COMPONENTS	OF VARIANCEPER	NCEPER	CENT				
Groups Stands/G	9 8 6	0 150	888	188	948	844	do 64	150 Pr	~ # &	000	0 0 0	F 0.3

Mean squares for seeds per cone were coded, x 0.1.

b This component was actually negative, but taken to be 0 here.

** Significant at the 1 per cent level. * Significant at the 5 per cent level.





in the collection from Collier County, Florida, and they decreased in diameter toward the north, east, and south. An east-west trough seemed to occur in the neighborhood of Polk County, Florida, and another extending southwest-northeast through the northern portion of the species range, with a minimum at Brantley County, Georgia.

The cone dimensions found here (Table 3) agree fairly well with values reported by others, as seen by the tabulation of "common" ranges below. However, it is obvious that these cone dimensions are not particularly useful for identifying varieties.

Authors	elliottii	densa	Both varieties
	Leng	thcentimete	rs
Small (1933, p. 4)	8-12	8-15	••
Coker and Totten (1937, p. 19)	•••	-	6-14
Little and Dorman (1954)	9-14	7-12	
Wakeley (1954, p. 198)	••		6-15
West and Arnold (1956, p. 5-6)	8-11	8-15	en en
Ward (1963)	•••	eo en	7-16
Present study (ranges among mother tree means)	8.2-15.5	7.0-15.1	7.0-15.5
	Diamet	ercentimet	ers
Little and Dorman (1954)	4-5	3.5-5.0	**
Wakeley (1954, p. 198)		••	3.3-4.6
Present study (ranges among mother tree means)	3-1-5-3	2.7-5.0	2.7-5.3

Seed yield

Seed yield was extremely variable both among mother trees (1 to 127 seeds per cone) and among stands (3 to 97 seeds per cone) (Table 3 and Fig. 9). Much of the variation among mother trees was associated with groups (22 per cent) and stands within groups (32 per cent) (Table 4). Variation among stand means fell into an irregular clinal pattern (Fig. 9). Some of the irregularity may be due to differences in stand density or similar factors not studied. A high occurred in an area centering at Thomas County, Georgia, with a moderately high ridge extending to the east and west. Yield usually decreased from this ridge both to the north and south, reaching an extremely low point at Big Pine Key, Florida.

Since seed crops generally vary from year to year, and since locality by year interactions are probable (Toumey and Korstian, 1942, p. 105), one should not assume that the pattern of seed yield per cone found here would be consistent in time.

The mean sound seed yield found for the whole species, 51 seeds per cone, is lower than that reported by Wakeley (1954), 60-70 seeds per cone. The discrepancy may be due to yearly effects as noted above, or to differences in the degree of winnowing.

Seed weight

The means of seed weight for mother trees were extremely variable (10 to 51 mg. per seed) (Table 3). Much of this variation was associated with stands and it exhibited a clear, mostly clinal pattern (Table 4 and Fig. 10). A northeast-southwest trough occurred in southeast Georgia extending from Pierce County to Evans County. Seed weight increased in

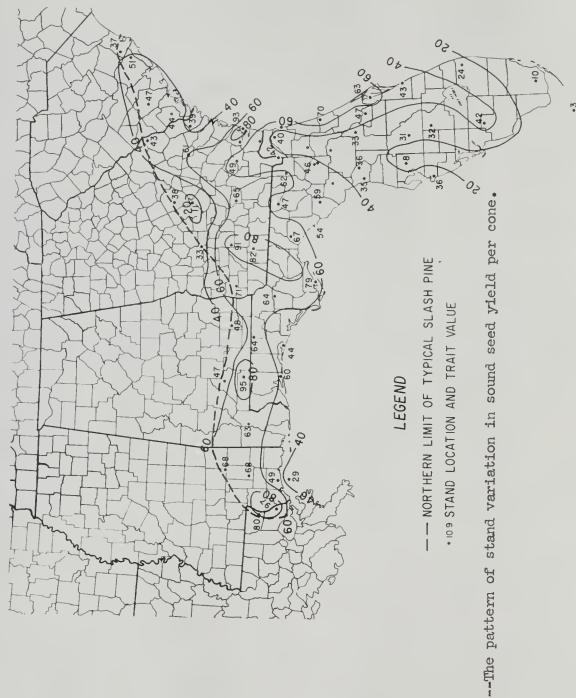
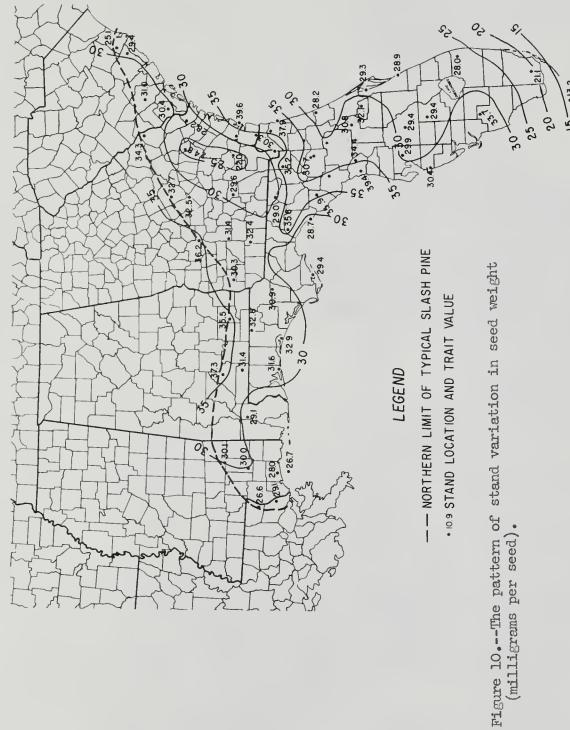


Figure 9. -- The pattern of stand variation in sound seed yield per cone.



all directions from this area. To the south, a northeast-southwest high occurred extending from Dixie County, Florida, to Duval County, Florida. It then decreased irregularly to the south. Note that the rate of change, however, was not uniform, the drop being the sharpest in south Florida.

The mean seed weight for all trees, 30.6 mg. (which converts to about 14,800 seeds per 1b.) agrees well with the ranges for slash pine given in the Forest Service Woody Plant Seed Manual (Anonymous, 1948, p. 269), 13,000 to 16,000 seeds per 1b. and also with the ranges of the means of 100-seed samples, 2.8-3.5 grams, given by Wakeley (1954, p. 198). Germinability and speed of germination

Germinability of seed varied highly among mother trees (6 to 100 per cent) (Table 5). Significant amounts of the variation were associated with stands and groups (17 and 6 per cent, respectively) (Table 6). Germinability averaged highest in the densa variety, next highest in the transition zone, and lowest in the typical variety. However, the pattern seemed to contain a large element of randomness and no isograms were drawn (Fig. 11).

The results agree with Mergen and Hockstra's (1954), in that significant differences among seed lots from different portions of the range of the typical variety were found and that no distinctive pattern occurred. However, the differences in germinability of seed from comparable areas in the two studies showed little agreement.

Germinability of seed may of course be affected by maturity at time of collection and other factors. Although attempts were made to collect only mature cones, there is no assurance that all lots were of the same degree of maturity. Hence, even though significant stand

Table 5.--Means and ranges of variation for progeny data of Nursery Test 2

Group	Germinability ^a	Speed of germination ^b	: Cotyledons
	Per cent	Per cent	Number
	M	ANS	
1 2 3	60.7 66.7	67.1	7-43
3	73.2	75 • 3 89 • 4	7.29 6.83
Ul groups	63.3	71.4	7.32
	RANGES AMO	ng seedlings	
1	49.49		4-12
2 3			4-13 4-10
	RANGES AMONG M	OTHER TREE MEANS	
1 2 3	6-96 23-94	0-99	6.0-9.4
3	14-100	7-100 5 3-1 00	6.2-9.3 5.5-8.0

a Per cent of sound seed germinating within 27 days after sowing.

b 15-day germination x 100. 27-day germination

Table 6 .-- Mean squares and estimates of variance components obtained from analyses of variance of progeny data of Nursery Test 2

1	: Germinability	Speed of germination	Cotyledons
	MEAN SQUARES		
Replications Groups Stands/G Error 1 Mother trees/S Error 2	5,027** 8,271* 1,704** 131 883** 86	135 25,163** 1,846** 407 978** 192	.199 17.743** 2.106** .087 .597**
ESTIMATED (COMPONENTS OF VARIAN	CEPER CENT	
Groups Stands/G Error 1 Mother trees/S Error 2	6 17 21 43 13	13 9 37 24 17	17 24 15 29 15

^{*} Significant at the 5 per cent level. ** Significant at the 1 per cent level.

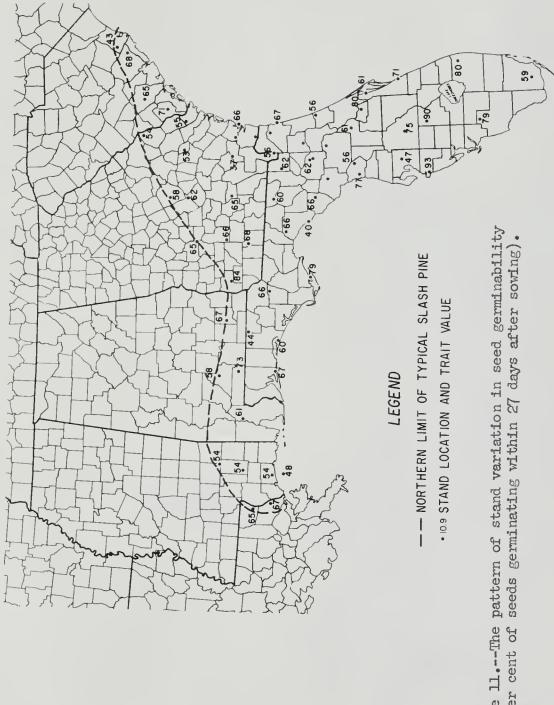


Figure 11. -- The pattern of stand variation in seed germinability (per cent of

differences were found they were not necessarily genetic in nature.

Speed of germination also varied greatly among mother trees (from 0 to 100 per cent) (Table 5). Significant proportions of the variation were accounted for by groups and stands (13 and 9 per cent, respectively) (Table 6). The stand variation exhibited a distinctive clinal pattern (Fig. 12). A low occurred in Ware County, Georgia, which also tended to extend westward to Holmes County, Florida, and Catalina Island, Mississippi, and northeastward to Georgetown County, South Carolina, as well. Speed of germination increased both to the north and to the south of the trough.

Evidence of racial variation in speed of germination has also been found in lodgepole pine (P. contorta Dougl.)(Critchfield, 1957), eastern hemlock (Tsuga canadensis (L.) Carr.) (Stearns and Olson, 1958), spruce (Picea) (Schell, 1960), and ponderosa pine (Callaham, 1959 and 1962).

Like germinability, differences in maturity of seed could have had some effect upon the differences in speed of germination among stands. However, the nature and distinctiveness of the trends practically rule out the possibility that such extraneous factors could have caused the pattern. More likely it was due to genetic differences in the seeds, brought about by natural selection and causing differential response to environmental stimuli.

It is of interest to speculate on the nature of the genetic differences that were apparently present, and on the particular environmental factors to which the seeds responded at the planting site. Past studies suggest that temperature is a major environmental factor. According to Callaham (1962), the speed of germination of tree seeds is

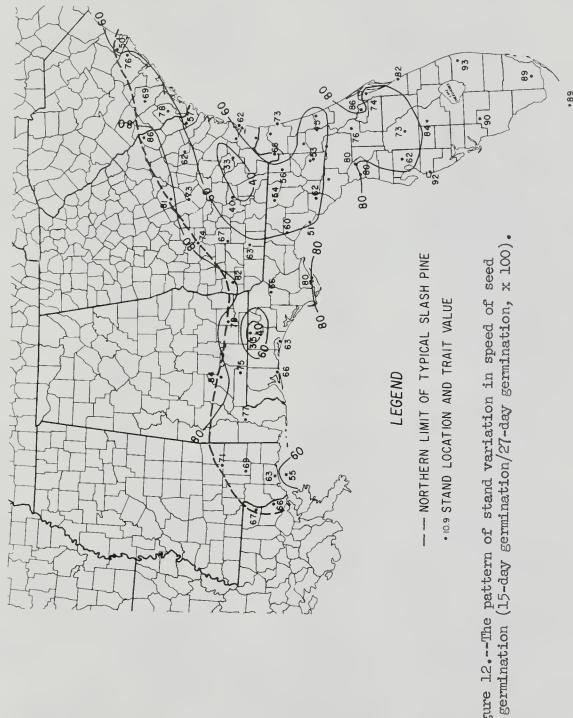


Figure 12. -- The pattern of stand variation in speed of seed

governed primarily by temperature, given adequate moisture and light, with germination proceeding most rapidly at some optimum temperature. Experiments by Jones (1961) suggest that photoperiod was not a predominant factor in causing the differences in rate of germination. He showed that a single exposure of slash pine seeds to 15 minutes of daylight doubled the total germination per cent over that obtained under complete darkness. But illumination periods of 8-, 12-, and 16-hours caused no differences in either speed of germination or total germination per cent.

Assuming that temperature was a major environmental factor, one might speculate that the seeds possessed different genetically-fixed optimum temperatures and this would be reflected in different rates of germination when the seeds were planted in a common environment. Such was found to be the case through laboratory tests by Callaham (1959 and 1962) for ponderosa pine. However, this alone would not explain why seeds brought north from south Florida and south from the northern limits to Olustee, Florida, germinated early.

Presence or absence of seed dormancy may have been important. In examining this possibility, it is well to review what is known about factors that may be involved. Most slash pine seed are shed in October (Cooper, 1957). Under natural conditions, seed tend to germinate in spring, but when soil moisture is adequate considerable germination may occur in early autumn (Derr, 1959). In south Florida, conditions for early fall germination would seem to occur rather frequently because October rainfall there averages about 6 inches. In contrast, October rainfall averages about 2 inches in the north. In the south, the winter months are dry (average rain about 2 inches per month) and relatively warm, while in the north they are wetter (about 4 inches per month) and considerably cooler.

Stored slash pine seeds show a mild degree of dormancy, germination being abetted by stratification, while fresh seed do not (Anonymous, 1948). These findings on dormancy were most likely based upon work with the typical variety of slash, although this point is not certain.

It is possible that dormancy may be more characteristic of northern seeds than southern seeds. In the north, if the seeds do not germinate promptly in the fall, there would likely have to be a mechanism built into the seeds to prevent germination over winter, because of the danger of cold temperatures to newly germinated seedlings. In the south, on the other hand, there would not seem to be a need for dormancy, because of the warm winters. In fact, it would seem that germination as early as possible after seed fall would carry a high selective advantage—prompt germination to avoid mortality from severe winter drouths.

The fact that northern seeds will germinate promptly under favorable conditions in the fall suggests that onset of dormancy (if it actually occurs) is delayed. Prompt fall germination undoubtedly carries a high selective advantage--trees germinating in the fall obtaining "a head start" on those germinating in the spring in regenerating denuded lands. However, prompt fall germination under suitable weather conditions plus dormancy when weather conditions fail would seem to be the best combination for the variety. These conjectures on dormancy are feasible in view of the findings with several forage species in Europe, in which it was shown that germination characteristics of species inhabiting different climates were closely tied in with dormancy mechanisms (Cooper, 1963).

Assuming both differential dormancy and different optimum temperature requirements, we might attempt to explain the results of the present study. South Florida seeds germinated earliest because they lacked dormancy. Seeds from south Georgia and north Florida germinated late because the stored seed possessed a mild degree of dormancy—had the seed been stratified differences may not have been found. Seeds from the extreme northern limits of the species range germinated promptly because, although they also may possess moderate dormancy, their optimum temperature was attained sooner, having been moved from a northerly to southerly direction. The latter conjecture assumes no difference in optimum temperature requirements within the northern region. Of course these are little more than guesses, further experimentation being necessary on this problem.

Cotyledon number

The number of cotyledons per seedling varied from as low as 4 to as high as 13 (Table 5). Much of the variation was associated with stands (24 per cent) and groups of stands (17 per cent).

Stand averages displayed a distinctive clinal pattern (Fig. 13) much like that for seed weight (Fig. 10). On the average, cotyledon numbers were higher in the north than in the south (Table 5). However, as seen in Figure 13, the pattern is much more subtle than this, with a low occurring in the north as well as in the south.

The means and ranges agree fairly well with previously reported values, as indicated in the following tabulation (means are followed by ranges in parentheses).

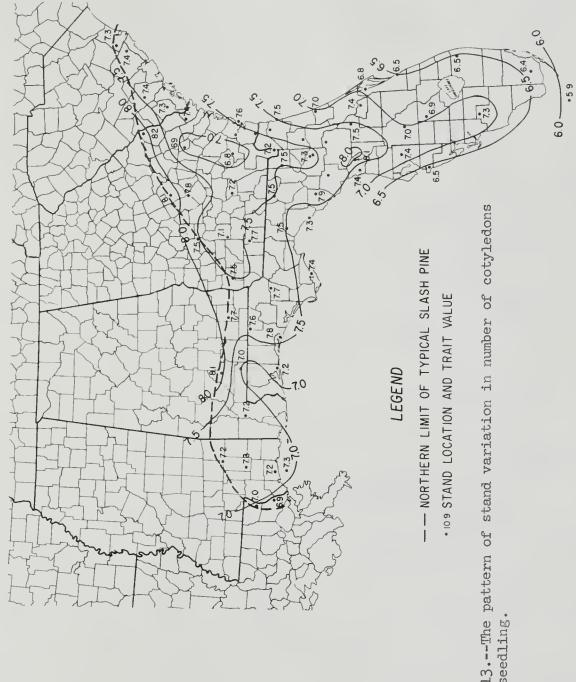


Figure 13.--The pattern of stand variation in number of cotyledons per seedling.

Author	elliottii	densa	Both varieties
	Num	bers of cotyledo	ns
Engelmann (1880, pp. 174, 186)	A.		8(6-9)b
Butts and Buchholz (1940)			7-73(5-10)b
Little and Dorman (1954)			
DeSoto National Forest, Miss.	7.36(6-9)		
Clinch County, Ga.	7.72(5-10)		
Hendry County, Fla.		6.76(5-8)	
Present study (ranges are among seedlings)	7-43(4-12)	6.83(4-10)	7-32(4-13)

- a Cited by Little and Dorman (1954)
- b Origin not specified

The correlation between cotyledon number and seed weight on a stand mean basis was .72, highly significant; the pooled correlation for mother trees within stands was .42, also highly significant.

Racial variation in respect to cotyledon number has also been found in loblolly pine (Thorbjornsen,1961). The positive correlation between seed weight and cotyledon number agrees with findings by Buchholz (1946) for ponderosa pine.

Total height

One-year-old seedling heights varied greatly and the majority of the variation (66 per cent) was associated with groupings of the stands. Seedlings in the northern portion of the species range were tallest (Tables 7 and 8, and Figs. 14 and 15). Variation in the north was relatively small but heights decreased rapidly going from north to south through Florida. Thus, the pattern is largely random in the north and clinal through Florida. There was also a modest east-west gradient

Table 7 .- - Means and ranges of variation for progeny data of Mursery Test 1

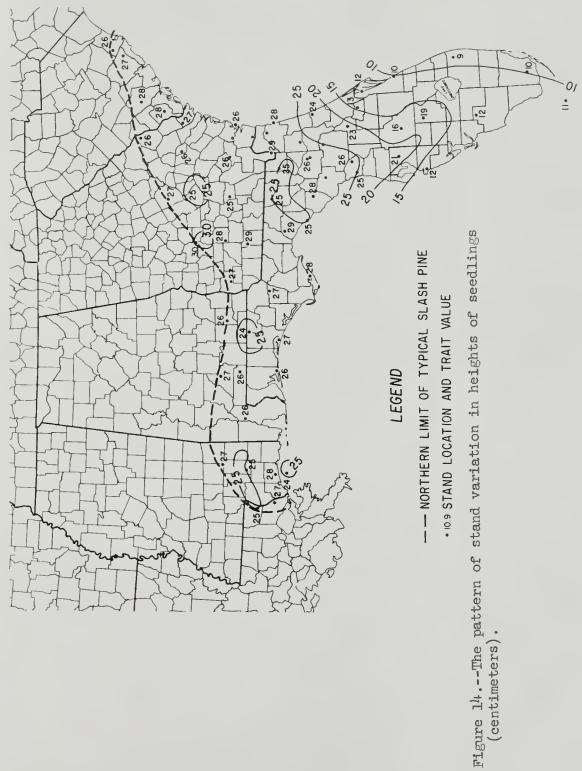
	: eter	diem- : per eter : fascicle	. length:	Sheath length	stomata per mm. of width	per mm. of length	Stomata per sq. mm.	Resin ducts	Hypo- derm layers
	Nm	Number	है।	8	Number	Mumber	Number	Number	Number
				MEANS					
26.7	19.5	88 89 49	17.2	826	5.5 5.4 8.5 8.5 8.5 8.5 8.5 8.5 8.5 8.5 8.5 8.5	0.000	53 469.0 148.8	24.5 33 8.5 8.5 8.5 8.5 8.5 8.5 8.5 8.5 8.5 8.5	1.52
0	1. T	2.84	15.8	•7•	5.83	8.9	51.9	2.40	1.49
		RAINCES	AMONG	NEEDLES OF	NEEDLES OR FASCICLES				
111	111	22-58	8-3 10-8 10-88	0.3-1.5	3.3-8.9	5.9-12.8 5.6-11.9 5.0-13.1	:::	000	4-
		RAINCES	RANCES AMONG SEEDLINGS OR	DILINGS OR	SEEDLING MEANS	EAIRS			
10-54	3-13 2-12 3-15	2.1-3.0 2.0-3.0	8-01 10-8 11-8	0.4-1.3	3.7-8.4	6.4-11.9	32-84	200-20	444
		RA	RANCES AVONG NOTHER-TREE MEANS	3 NOTHER-T	THEE MEANS				
18-35	5-9	2.6-3.0	12,19	0.6-1.1	4.6-7.0	8.0-10.0	38_65	1.8-3.0	0,[-[-
30	6-9	2.6-3.0		0.7-0.9	4.9-6.4	8.0-9.5	40-58	0 0 0 0	13-16
2	11-9	2.2-2.9	14-21	0.6-1.0	4.9-6.7	7.6-9.7	43-60	0.0-0.0	91-01

Banges are among seedlings for total height and stem diameter, and among seedling means for all other traits.

Table 8.--Mean squares and estimates of variance components obtained from analyses of variance of progeny data of Mursery Test 1

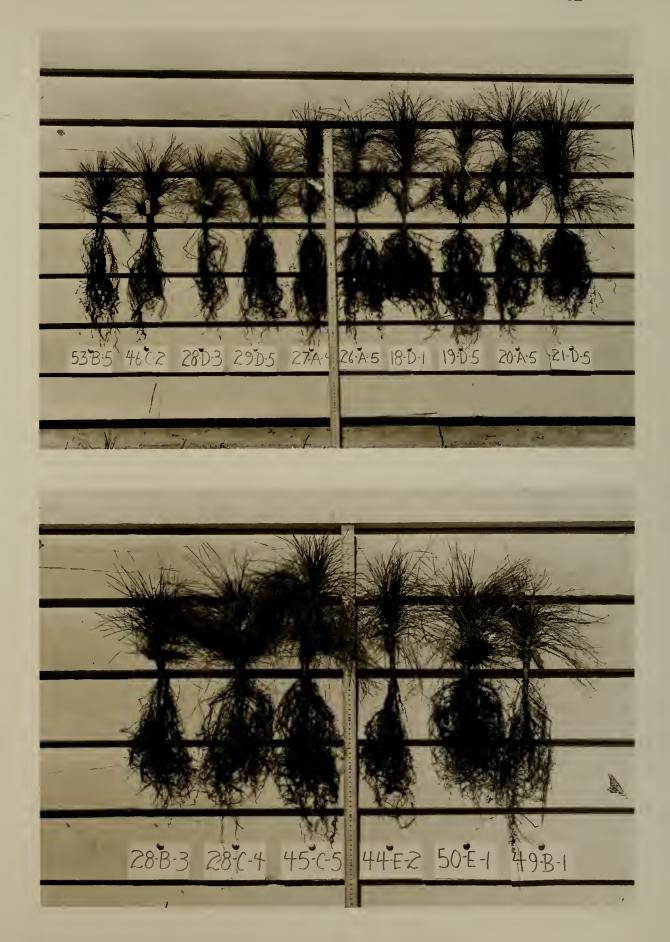
Source of variation	Total: height	Stem diam- eter	Needles per fascicle	Needle length	Sheath length	Rows of :Rows of :stomata :per mm. :per mm. of width:of length	ns of :Rows of :nmata :stomata :nm. :per nm.	Stomate per sq.	Resin ducts	Hypo- derm	
				MEAN SQUARES	QUARES						
Replications Groups Stands/G Mother trees/S Error	17,824.** 17,824.** 156.** 39.**	168.3* 168.3* 1.0.00	0.16** 5.13** .05**	163.0** 980.6** 17.0** 5.6**	.146** .086** .027**	2.86** 6.10** 1.14* 1.42* 1.42*	0.50 17.57** 1.18** .72* .59	2,096** 136** 136** 13**		**17.1	
		ESTIN	ATED (COMPONEMES	OF VARIANCE	PER	CENT				
Groups Stands/G Mother trees/S Error	66 7 4 59	8000G	30 50 40 50 50	幸の心だ	-108	6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6	80 th 40 th	140E	444	100 76	

* Significant at the 5 per cent level. ** Significant at the 1 per cent level.



(centimeters)

Figure 15.--One-year-old slash pine seedlings, showing differences in total height and stem diameter. Upper photo represents a latitudinal transect through the species range, the one on the extreme left being from Big Pine Key, Florida, and the one on the extreme right from Sumter County, Georgia. Lower photo shows differences between trees from the west coast (the two trees on left), the interior (center two), and the east coast (the two on right) of central Florida.



through central Florida, seedlings being tallest in the center of the state, and shortest along the coasts.

In a general way these results are in harmony with Little and Dorman's (1954) use of stem height as a diagnostic feature for identifying varieties. However, because of the gradient in Florida it apparently would be difficult to classify seedlings in the transition zone.

The fact that seedlings in the north-central region were not particularly taller than those at the extremities of the north, seems to disagree with findings by Squillace and Kraus (1959). However, seeds were relatively small and germination relatively late in the north-central region. These two factors apparently had some effect upon heights. The within-stand pooled correlation coefficient between seedling height and seed weight was .31 (significant at the 1 per cent level) and between seedling height and rate of germination, .17 (significant at the 5 per cent level).

On the other hand, the superiority in early height growth of trees from the north to those of the south is great enough to be real in spite of seed weight and rate of germination effects. Reasons for this difference probably lie in the fact that the south generally suffers from extremes of climatic and other environmental conditions more so than does the north. Such factors could include poor rainfall distribution with frequent droughts in spring and flooding in summer, damaging tropical storms, and possibly frequency of fires. In the south, natural selection is probably relatively strong for resistance to these factors, which may cause relatively weaker selection for rapid growth than in the north.

Admittedly there are also climatic extremes in the peripheral portions of the north. For example, relatively cold temperatures and frequent ice storms are characteristic of the area just south of the northern limits; tropical storms are relatively frequent along the Gulf coast; rainfall distribution is relatively unfavorable along the coasts of Georgia and South Carolina; conditions conducive to fusiform rust damage seem to be most favorable at the northern extremities (McCulley, 1950).

The east-west gradient through much of Florida may be associated with the difference between mean maximum and mean minimum daily temperatures (Fig. 3)—trees tend to be tall where the temperature difference is relatively high. This possible association is supported by findings reported by Kramer (1957) and Hellmers (1962)—in laboratory tests loblolly pine and northern red oak (Quercus rubra L.) grew fastest under the greatest day-night temperature differential tested.

Stem diameter

Variation in stem dismeter showed a moderately high racial component (25 per cent for groups and 6 per cent for stands within groups) and the stand means exhibited a clinal pattern (Table 8 and Fig. 16). Stems were thickest in the South Florida seedlings and they decreased rather uniformly to a northeast-southwest low extending from Taylor County, Florida, to Liberty County, Georgia. North of this trough, diameters increased slightly, but were not as large as those from south Florida. Stems usually were thicker (especially relative to height) along the coasts of Florida than in the interior.

Thick stems are an indication of a carrot-like taproot. Thus, in a general way, the results agree with Little and Dorman's (1954) use of

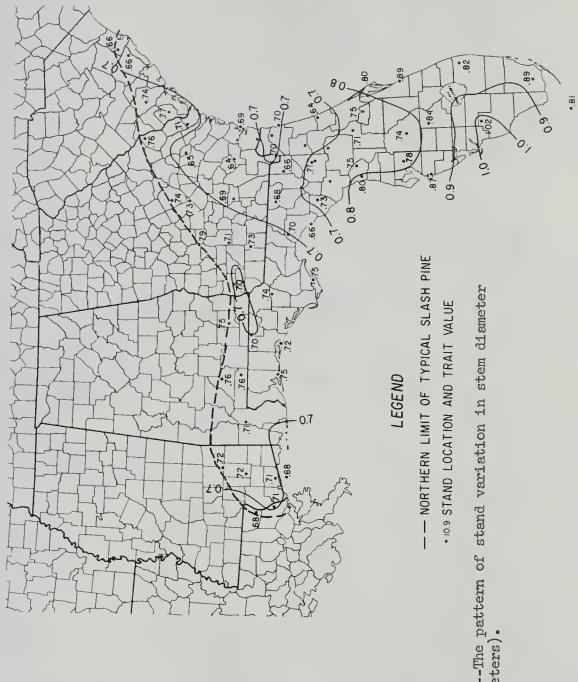


Figure 16.-- The pattern of stand variation in stem diameter (centimeters).

this trait as a diagnostic feature. Stands in groups 1, 2, and 3, averaged 7.1, 7.4, and 8.5 cm., respectively. Trees from stands near the northern limits of the species range had moderately thick stems but they were taller than South Florida seedlings and hence would not detract from diagnostic utility of this trait. However, like total height, the difficulty is that because of the clinal nature of the pattern it would apparently be difficult to classify trees or stands in the transition zone.

Thickness of stem in slash pine seedlings has undoubtedly been important in natural selection. South Florida seedlings, which characteristically have thick stems, are more resistant to fires than north Florida seedlings (Ketcham and Bethume, 1963). Apparently, this thickening of the hypocotyl, which is mostly dead outer bark but also inner bark and wood, imparts a degree of insulation against heat (Little and Dorman, 1954). The thick stem also probably provides a means for storing food, utilizable for sprouting when the crown burns. Hence, the trait is assumed to have resulted as an adaptive response to fire (Little and Dorman, 1954).

If the trait is an adaptive response to fire, one would expect that the frequency of natural fires, or the extent of damage from fires, increases gradually from north to south, following the pattern of variation in stem thickness. No concrete and reliable data could be found to check this possibility. However, as noted earlier, slash pines in the north were originally restricted to ponds, pond margins, and other wet areas. Hence, it is possible that fires in the south invaded slash pine stands more frequently, and perhaps were more intense, than in the north. Extended

late winter and early spring drouths and high winter temperatures, common in the south, may be factors affecting the frequency and intensity of fires.

Regressions were calculated to determine factors that might have been involved in the apparent natural selection on stem diameter. Stem diameter (stand means in centimeters, Fig. 16) was used as the dependent variable. Independent variables used were as follows: (1) latitude (stand values in degrees); (2) the sum of precipitation-evaporation (P-E) ratios for months of February through April (stand values, Fig. 6); and (3) mean January temperature (stand values in OF., Fig. 2). P-E ratios (used as a measure of late winter-early spring drouth) and January temperature were considered as possible environmental factors causing natural selection. Latitude in itself could not, of course, cause natural selection, but the variable was included to test the apparently strong latitudinal trend and to see if effects of P-E ratios and temperature, independent of latitude, could be shown. The analyses included simple, multiple, and curvilinear regressions. Results are shown below.

Simple Regression Analyses

Stem diameter (Y) on:	Regression coefficients	Coefficients of determination
		Per cent
Latitude (X ₁)	0232	40.1**
FebApr. P-E ratios (X2)	0042	15.6**
Jan. temperature (X3)	•0090	36.7**

Multiple and Curvilinear Analyses

Stem diameter (Y) on:	Standard partial regression coefficients	Coefficients of determination
•		Per cent
X1 and X2	615,031	40.2**
x ₁ and x ₃	702,072	40.1**
X1, X2, and X3	-1.111,205,621	40.8**
x_1 and x_1^2	-6.649, 6.000	48.1**
X ₃ and X ₃ ²	-2.765, 3.385	46.8**

** Significant at the 1 per cent level

In the simple regression analyses latitude showed the strongest relationship to stem diameter, as indicated by the coefficients of determination. This suggests that some environmental factor, correlated with latitude, was instrumental in causing the stem diameter pattern. The regression coefficient for temperature was almost as strong as latitude, while that for P-E ratios was considerably weaker, but still highly significant. Multiple regressions showed no significant increase in the variance accounted for (indicated by the coefficients of determination) over and above that accounted for by latitude alone. This was due to high intercorrelations between the independent variables. Therefore, there is no proof that either temperature or P-E ratios had effects independent of latitude. Because of the reversal in trend of stem diameter in the north-central area, curvilinear regressions were tried for latitude and temperature. Both regressions accounted for significantly (1 per cent level) more of the variance above that accounted for by respective linear regressions. However, latitude still was superior to temperature.

From the analysis we can only conclude that the latitudinal trend in stem diameter, with a reversal in the north-central area, was significant. Temperature and P-E ratio may have had some real association with the trend, but some other environmental factor must also be involved. Needles per fascicle

Both binate and ternate fascicles were found in the parental samples. but the relative frequencies varied considerably as indicated by average numbers of needles per fascicle (Table 3). Stand differences displayed a very distinctive pattern, with a north-south high in extreme southeast Georgia and northeast Florida, and another northwest-southeast high in north-central Florida (Fig. 17). Needles per fascicle usually decreased gradually away from these highs. A notable feature was that, although numbers were low in south Florida, they were also usually low at the extremities of the species range. Thus, the results do not agree well with Little and Dorman's (1954) recommended use of this character for separating varieties -- differences in sampling technique may have caused the disagreement. Average number of needles per fascicle in the progenies was generally higher than in the parents (Table 7). This may be due to an effect of tree age, or to the fact that the progenies, being grown in a nursery, had a more favorable environment than trees under natural conditions. A very few progeny fascicles contained four needles and one contained five.

The pattern of variation among stands in the progenies was somewhat similar to that in the parents (Fig. 18). However, the two pronounced highs found in the parents were less noticeable in the progenies and also the difference between south Florida and the remainder of the species range was more pronounced in the progenies.

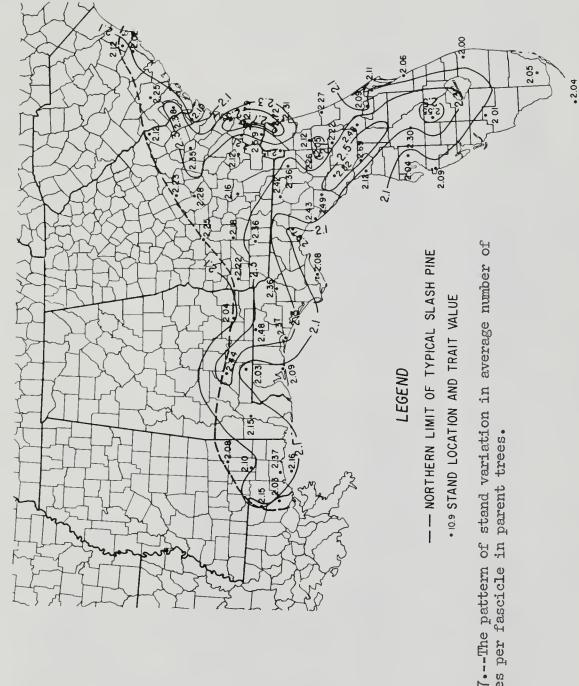


Figure 17.--The pattern of stand variation in average number of needles per fascicle in parent trees.

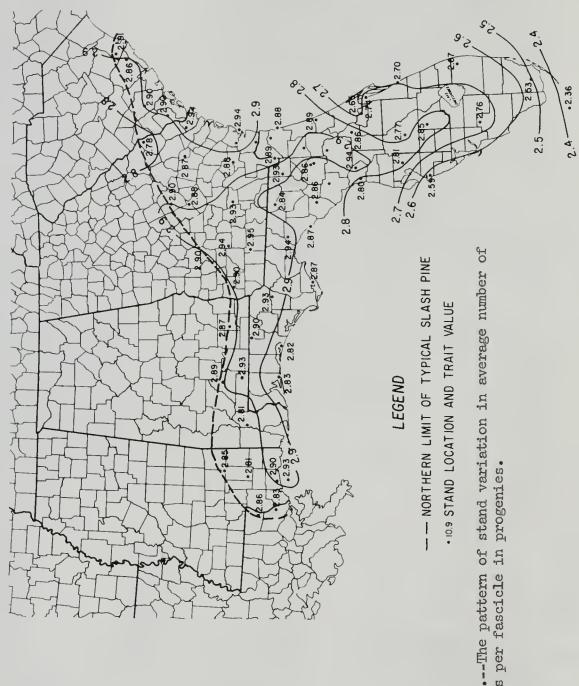


Figure 18.--The pattern of stand variation in average number of needles per fascicle in progenies.

The pattern of variation in both parents and progenies seems to be, in some respects, associated with severity of environment. The low in south Florida coincides with unfavorable distribution of rainfall and the low in the extreme north is associated with cold winter temperatures. Somewhat similar trends have been reported for ponderosa pine. Needles per fascicle in ponderosa pine tend to be low in eastern portions of the species range (Weidman, 1939; Haller, 1962; and Wells, 1962), where the climate is relatively severe and the trees are generally slower growing. The results agree with Shaw's (1914) statement that in some species of trees the number of needles per fascicle is dependent upon climatic conditions, smaller numbers occurring in colder regions.

The apparent relation of needles per fascicle and severity of climate may be associated with photosynthetic efficiency. It can be shown that a ternate fascicle has about 20 per cent more leaf surface area per unit of needle volume than a binate fascicle of the same diameter and length. Thus, a ternate fascicle, having more surface area for absorption of light and for exchange of gases per unit of chlorophyll-bearing tissue, may be more efficient photosynthetically than a binate one. A binate type, on the other hand, would seem to be an adaptation for conserving moisture loss or for frost hardiness, at the expense of growth efficiency. High frequency of ternate fascicles then may be an adaptation to vigorous growth in optimum climate while a tendency toward a preponderance of binate ones an adaptation to less favorable climate. These possibilities would seem to be worthy of further study.

Needle length

Needle length in the parent trees exhibited a rather complicated pattern of variation among stands (Fig. 19). In general, needles averaged longer within the range of variety densa than in the north (Table 3). However, the tendency was not uniform, highs occurring in the north as well as in the south. Needles tended to be relatively long in the coastal areas, suggesting a possible tie-in with the difference between mean minimum-mean maximum temperatures (Fig. 3). But the correlation coefficient between these two variables was nonsignificant (r = -.23).

The pattern in the progenies was simpler, containing a strong element of clinal variation (Fig. 20). Needles were generally long in south Florida (excepting at the extreme tip) and they decreased northward to a northeast-southwest low through south Georgia, and then increased above this area. The pattern vaguely resembles that in the parents in that needles were, on the average, longest in the south (Table 7).

The ranges in lengths of needles for parent material are compared against those shown by others below.

Author	elliottii	densa	varieties varieties
		Centimeter	
Harlow (1931)			15-30
Small (1933, p. 4)		18-30	
Coker and Totten (1937, p. 19)			15-23ª
West and Arnold (1956, p. 5-6)	18-30	18-30	
Present study (ranges among mother tree means)	15-27	18-31	15-31

a Rarely, 10-25

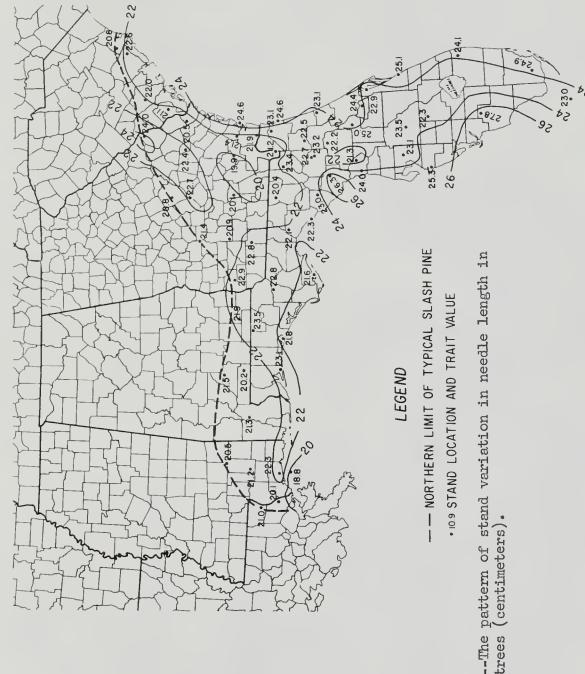


Figure 19.--The pattern of stand variation in needle length in parent trees (centimeters).

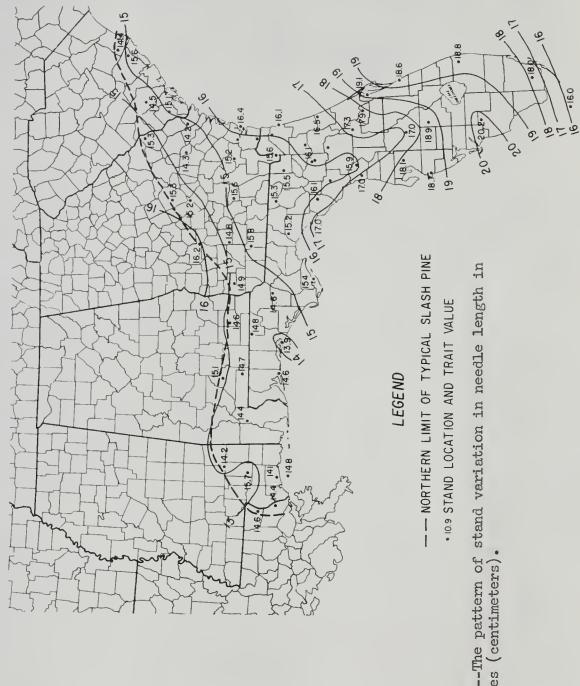


Figure 20.--The pattern of stand variation in needle length in progenies (centimeters).

Fascicle sheath length

Variation in fascicle sheath length in the parental data was strongly associated with stands, none of it being associated with groups (Table 4). But the pattern of stand variation was rather intricate (Fig. 21). A significant feature was that a pronounced north-south low occurred through the center of Florida and southeast Georgia.

In the progenies the stand component of variation was significant but rather small, 11 per cent (Table 8). Stand means displayed no particular trends, with a large element of randomness (Fig. 22).

The ranges of variation in sheath length found in the parental data do not agree very well with reports by others as seen below. The discrepancies may be due to differences in maturity of the foliage sampled, or to differences in technique of measurement (such as inclusion or exclusion of frayed ends).

Authors	elliottii	densa
	Centime	ters
De Vall (1941a)	0.8-1.3	1.0-1.4
West and Arnold (1956, p. 5-6)	1.3 and under	1.6
Present study (ranges are among mother tree means)	1.2-2.3	1.1-2.3

De Vall (1940) considered fascicle sheath length to be very diagnostic, it being unaffected by climate, soil type, tree age, etc., and that the character was useful to separate slash and longleaf pine.

Stomatal measurements

Results of the three measures of stomatal frequency were similar in that (1) in the parental data only small amounts of variance were associated

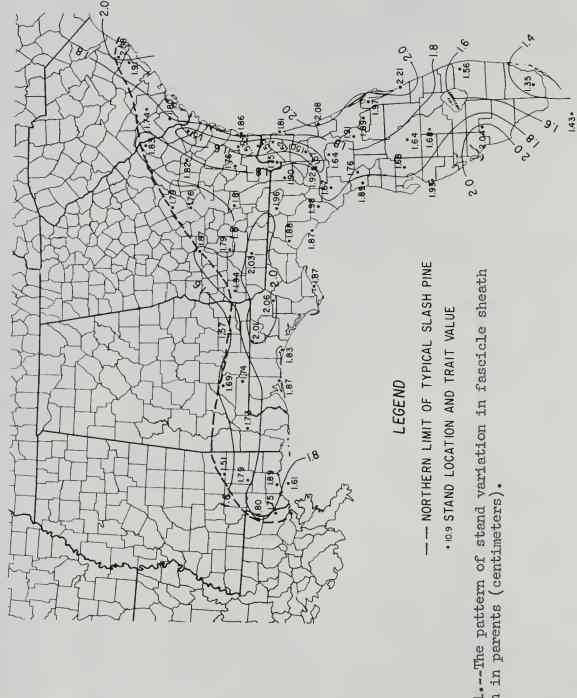


Figure 21. -- The pattern of stand variation in fascicle sheath length in parents (centimeters).

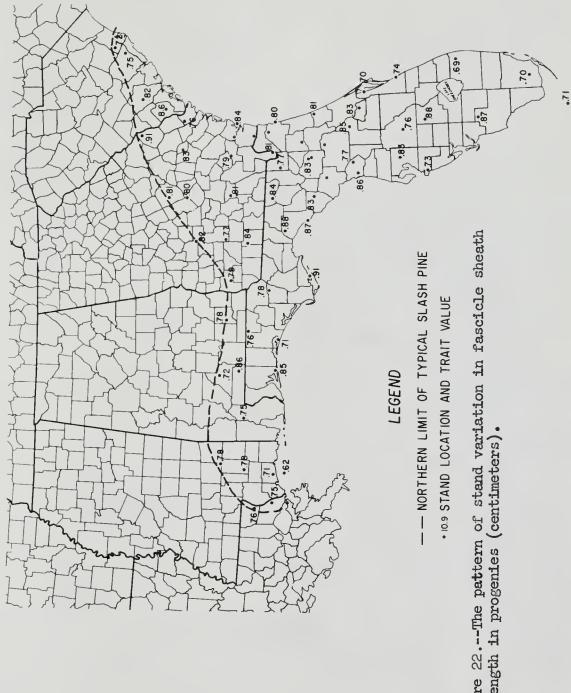


Figure 22. -- The pattern of stand variation in fascicle sheath length in progenies (centimeters).

with groups or stands, with the patterns of the stand means being largely random; and (2) in the progenies it was possible to show patterns for the stand means, although they were somewhat erratic (Figs. 23 through 28). A common feature was a tendency for stomatal frequency (all three types of measurements) to average relatively high in the north and low in the south, and also some tendency for a high to occur in the north-central area.

Mergen (1958) found a clinal pattern for stomata per mm. increasing from west to east in slash pine progenies from 12 sources encompassing much of the northern part of the species range in Georgia and Florida. The pattern was curvilinear, however, with most of the variation occurring in the east. His pattern is only vaguely apparent in the progeny data of the present study—a high occurred in east Georgia but another high occurred in the extreme western portion of the species range.

Thorbjornsen (1961) found geographic variation in stomata per mm.

in natural stands of loblolly pine. His pattern was somewhat similar to

Mergen's, frequency tending to be highest in the eastern part of the range.

But the trend was not uniform, the pattern appearing to be somewhat random

east of the Mississippi river. He also found a rather strong positive

correlation of stomata per mm. with a drought index, the ratio of May
August precipitation over average summer temperature. A check for a

similar relationship was sought in the present data for slash pine, with

no success—if anything there was a slight negative trend. Apparently

the relationship Thorbjornsen found was mainly due to the very low

summer rainfall west of the Mississippi being coincident with low stomatal

frequency in that area. If so, the lack of a relationship for slash pine

is not surprising.

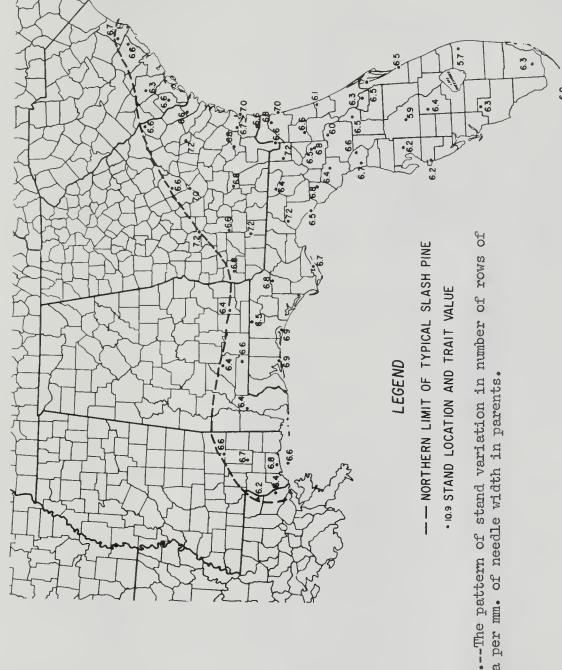


Figure 23.--The pattern of stand variation in number of rows of stomata per mm. of needle width in parents.

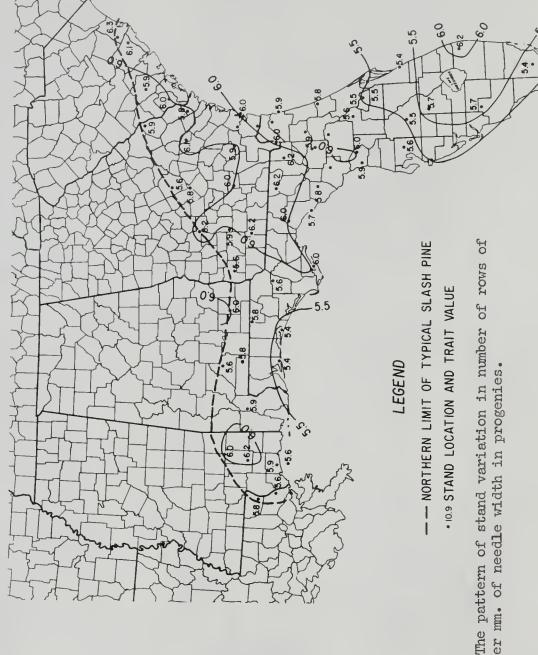


Figure 24..-The pattern of stand variation in number of rows of stomata per mm. of needle width in progenies.

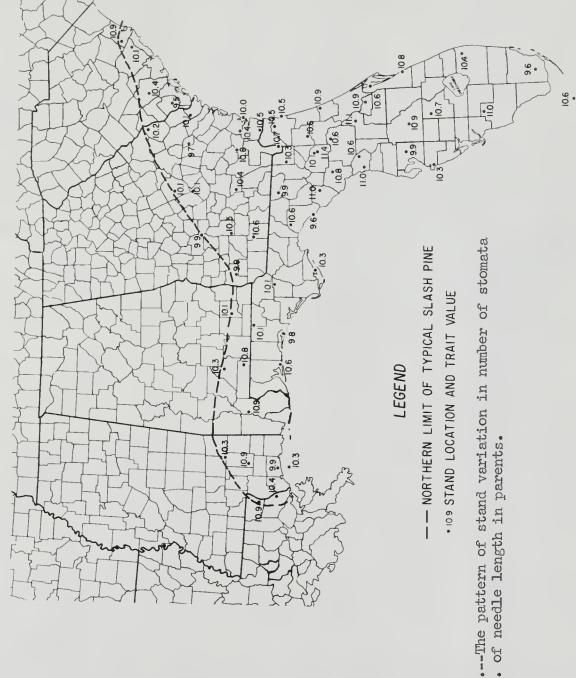


Figure 25. .- The pattern of stand variation in number of stomata per mm. of needle length in parents.

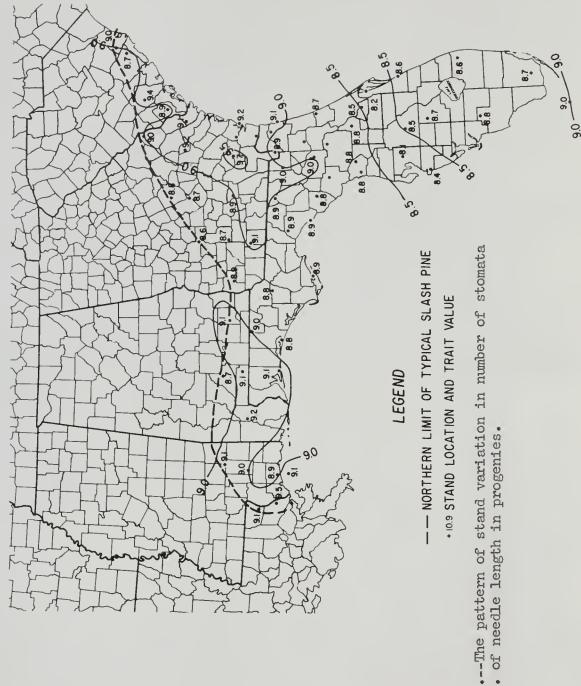


Figure 26.-- The pattern of stand variation in number of stomata per mm. of needle length in progenies.

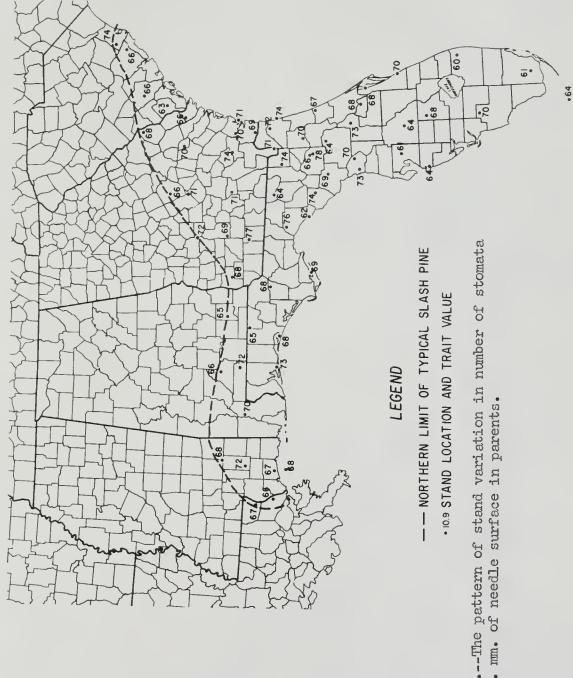
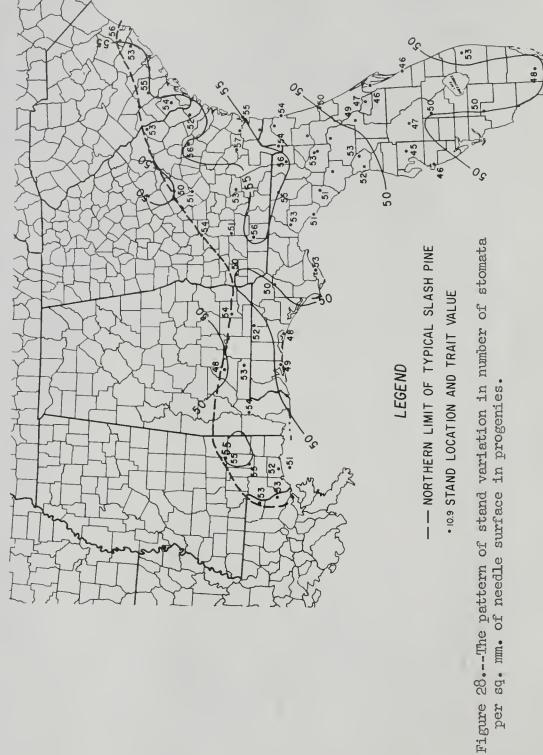


Figure 27.--The pattern of stand variation in number of stomata per sq. mm. of needle surface in parents.

•52



per sq. mm. of needle surface in progenies.

Thames (1963), sampling loblolly pine seedlings originating from areas in Caldwell and Cherokee Counties, Texas, northwest Georgia, and Crosett, Arkansas, found stomatal frequencies (both stomata per mm. and stomata per sq. mm. of needle surface) to be lowest in the two Texas sources, which agrees with Thorbjornsen's results. Although there were only two sources east of the Mississippi the two traits showed no consistent east-west trend in this region.

Thames (1963) found no significant racial difference in number of rows of stomata in loblolly pine and this was also found to be true for provenances of European larch (Larix decidua Mill.) (Gathy, 1959).

Low stomatal frequency may be an adaptation to xeric conditions as suggested by Thames (1963). High stomatal frequency may be associated with photosynthetic efficiency as found in Ribes by Bjurman (1959).

Number of resin ducts

The number of ducts in parental foliage averaged 6.90 per needle, ranging from 2 to 13 among individual needles, and from 3.0 to 10.2 among mother tree means (Table 3). Trees of the densa variety averaged slightly more ducts than those of the elliottii variety or those in the transition zone, but the differences attributable to such groupings were not significant (Table 4). Stands-within-groups was significant but accounted for only 9 per cent of the variance. The pattern among stand means was rather intricate, highs occurring in south-central Georgia, and also along the coasts of Florida (Fig. 29). The low in extreme southeast Florida agrees with data reported by De Vall (1941b).

The high mother tree component (89 per cent) may be largely due to environmental modification rather than to genetic differences among

2.0 •

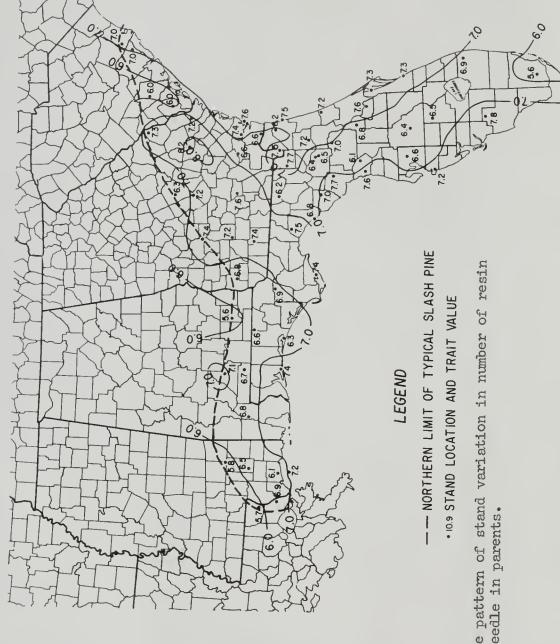


Figure 29.--The pattern of stand variation in number of resin ducts per needle in parents.

pine (Pinus serotina Michx.) was related to tree age, growth rate, vertical position in crown, and "crown exposure side." Their findings suggest further that even the stand variance may be due to environmental modification rather than racial effects.

In the progenies the numbers of ducts were much fewer, averaging 2.40 and ranging from 0.0 to 5.0 among seedling means (Table 7). Complete absence of ducts was extremely rare, being found in the sample of two needles from a single seedling. "Twos" and "threes" were the most common.

Very little of the variation in progenies was associated with groups or stands, error accounting for most of it (Table 8). The pattern of variation among stand means was largely random (Fig. 30). These results do not agree well with those of Mergen (1958), who found that slash pine seedlings from the central and northeastern counties of Florida and southeastern Georgia had the fewest ducts.

The absence of a distinct difference in number of resin ducts in parental foliage between the varieties of slash pine agrees with Little and Dorman's (1954) findings, but not entirely with those of others as indicated in the tabulation below.

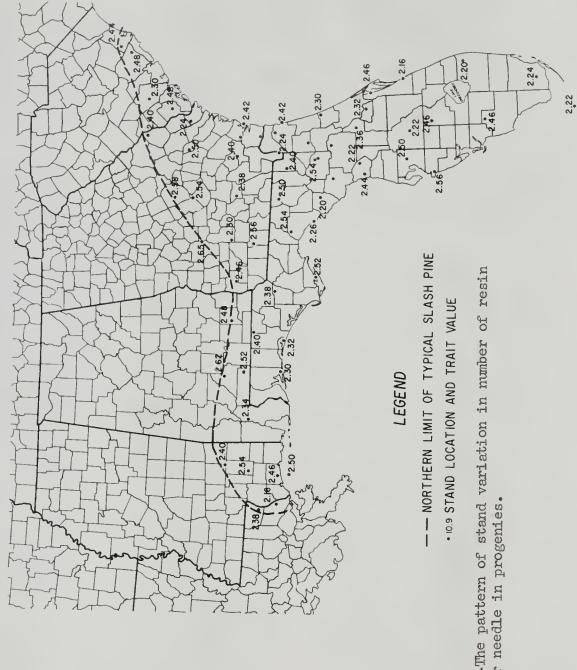


Figure 30.---The pattern of stand variation in number of resin ducts per needle in progenies.

Author	elliottii	densa
	Numbers	of ducts
De Vall (1941a)	3-5	4-9
De Vall (1945)	2-3ª	4-9ª
Little and Dorman (1954)	2-8 ^b	3-9 ^b
West and Arnold (1956, p. 6)	3-4	5-10
Present study (ranges among mother tree means)	3-10	4-9

- a Resin droplets visible with a hand lens on a cut surface in this case.
- b For natural stands; the authors showed generally fewer ducts for plantations, which may have been an age effect.

Thickness of hypoderm

Although the thickness of hypoderm in the parents averaged only slightly greater in the <u>densa</u> variety than in <u>elliottii</u> the differences were significant, 37 per cent of the variance being associated with groups of stands (Tables 3 and 4). The stand means displayed a clinal pattern, increasing from north to south, through much of Florida and a random one in the north (Fig. 31).

In the progenies the results were completely different. Groups and stands accounted for relatively small (although significant) portions of the variation, 7 per cent each (Table 8). North Florida progenies had slightly thicker hypoderms, on the average, than south Florida ones (Table 7). But the over-all pattern of stand means showed no clear cut trends, and contained a large element of randomness (Fig. 32).

The outer, thin-walled hypoderm layer was invariably present in both parent and progeny material. In the parents at least one fairly continuous,

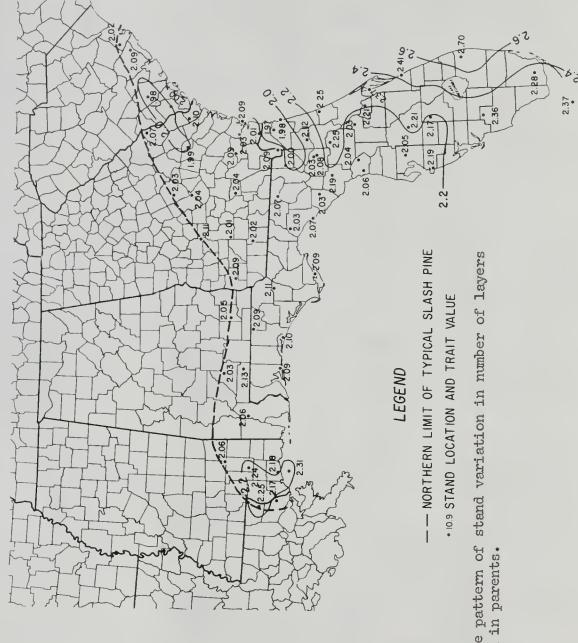


Figure 31. -- The pattern of stand variation in number of layers of hypoderm in parents.

1.50 •

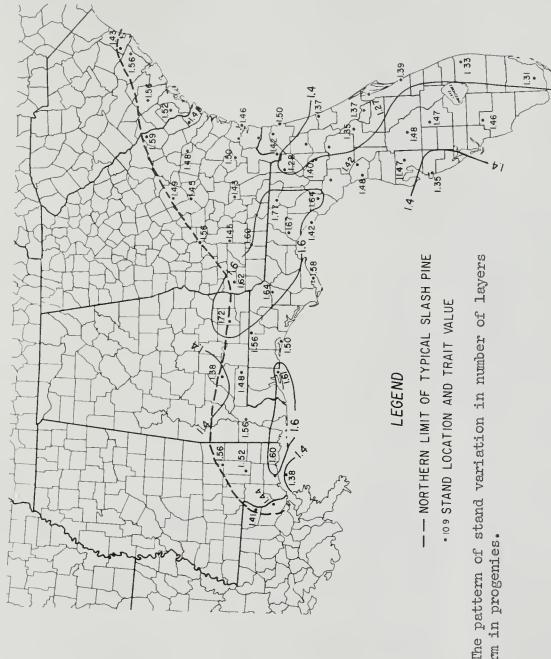


Figure 32. -- The pattern of stand variation in number of layers of hypoderm in progenies.

inner, thick-walled layer was present. In the progenies, however, the inner "layer" often consisted of sporadic thick-walled cells.

The results for parent trees agree fairly well with Dorman and Little (1954), although the magnitude of the differences they reported between elliottii (two, rarely three layers) and densa (three to four, rarely two or five) were greater than found here (Table 3). This may have been due to the fact that only current year's needles were used in the present study. The poorly developed hypoderm found in seedlings is probably an age effect. Because of this one should not conclude that the variation in thickness of hypoderm in mature trees is not genetic in nature. In a racial variation study with ponderosa pine, Weidman (1939) did find that geographic differences in this trait were inherited to a large extent.

Little and Dorman (1954), who studied Caribbean pine as well as slash pine, suggested a possible tie-in with climate, thick hypoderm being associated with a dormant dry season for these subtropical and tropical pines. In ponderosa pine thick hypoderm seems to be associated with severe climates (Weidman, 1939).

Discussion of Individual Trait Variation

At this point the individual trait patterns and the components of variance found in the analyses shall be summarized, and the causes and nature of the patterns shall be explored from the genetic standpoint.

Six of the 12 traits studied in the parents and 11 of the 13 studied in the progenies showed significant differences (either at the 5 or the 1 per cent level) among groups of stands. The prevalence of these differences was not surprising since they encompassed the whole species

range and in some instances reflect varietal differences.

However, 10 of the 12 parental traits and 12 of the 13 progeny traits studied showed significant differences among stands within groups. Thus, geographic variation (both phenotypic, as evidenced by parental traits and genetic, as evidenced by progeny traits) seems to be the rule rather than the exception in slash pine, even when considering the varieties as separate taxonomic entities.

In some traits, variation associated with location of the stands was relatively high and in others it was low. Here we are considering variation over the whole species range, which is expressed by the magnitude of the group and stands-within-groups components of variation, taken together. In the parents, this total stand-to-stand variation was relatively high for cone dimensions, seed yield and weight, needles per fascicle, needle length, sheath length, and hypoderm thickness; it was relatively weak or absent for stomatal measurements and resin ducts. In the progenies, total stand-to-stand variation was high for total height, stem diameter, needles per fascicle, needle length, speed of germination, and cotyledon number, while such variation was relatively weak for sheath length, stomatal measurements, resin ducts, and hypoderm thickness. Germinability also showed strong differences associated with locality of source but variation, in this case, may not have been genetic.

The patterns of stand-to-stand variation differed among traits but most of them showed continuity in one form or another. Seven of the traits showed clear, clinal trends with a single distinct reversal: cone length, seed yield, and seed weight in the parents; speed of germination, cotyledon number, stem diameter, and needles per fascicle in the progenies.

Nine others also showed continuity, but the trends were rather highly fluctuating and sometimes intricate, with two or more reversals: cone diameter, needles per fascicle, needle length, fascicle sheath length, and resin ducts in parents; needle length, rows of stomata, stomata per mm., and stomata per sq. mm. in progenies. Two traits showed a random pattern in the north and a clinal trend in the south: hypoderm thickness in parents and total height in progenies. Five showed statistically significant differences among groups and/or among stands within groups but no distinct geographic trends or ecotypes were apparent: rows of stomata and stomata per mm. in parents; germinability, fascicle sheath length, and hypoderm thickness in progenies. Finally, two showed no significant stand differences: stomata per sq. mm. in parents and resin ducts in progenies.

As was also indicated above, the patterns contained reversals, where clinal trends changed direction. These were evidenced by definite "highs" or "lows" within interior portions of the species range. In approximately half of the traits a reversal occurred in the north-central region. Some traits showed several clearly defined reversals. Since clinal trends were associated with these, and since this type of variation likely results from adaptation to continuous environmental factors, the reversals were taken to be indications that two or more environmental factors were involved in causing the pattern and that interactions and/or curvilinear effects occurred. For example, winter temperatures may have a strong effect on a particular trait in the extreme north, with only a weak effect in the south. The opposite could be true for winter precipitation and if both of these factors affected a single trait a reversal could occur-

It is pertinent at this point to consider the nature of the clinal patterns from the genetic standpoint. Natural selection operates on individual traits, and, in doing so, it changes the gene frequencies at the loci involved. Different selection pressures in different portions of the species range then may cause differences in gene frequencies (Dobzhansky, 1951, p. 176).

Thus, considering a particular trait, a clinal pattern may be viewed as a gradient in frequencies of the gene or genes affecting that trait. As a result of the gradient in gene frequencies there will be a similar gradient in genotypic frequencies. In other words, although it may sometimes be convenient to consider a cline as a gradually changing "type tree," it is more realistic to consider it as a gradual change in the proportion of the different possible types of individuals. Of course, if the trait under consideration is affected by a number of genes and/or if environmental effects occur, various intergrades may be found.

A consequence of this situation is that unless complete fixation, or "loss of genes," has occurred in one or more areas, one can expect to find deviant individuals in all parts of the species range. An example seems to be available in slash pine--Perry and Wang (1957) found that about 4 per cent of seedlings in a South Florida slash pine nursery bed did not show a "grass stage" and that various intergrades were present. If the interpretation of a cline, based on a gradient in gene frequencies, is correct then one should be cautious in speculating on the origin of deviants--they may frequently be just as much a part of the population in the area found as are normal seedlings.

The magnitude of genetic variation among trees within stands vs.

that due to stand location is of particular interest to tree improvement
workers—the comparison is important in judging the relative merits of
within stand and between stand selection. The parental data are of
little value in considering this question because the estimated components
of variance contain environmental effects along with genetic ones and
the two kinds cannot be separated.

The progeny data, on the other hand, can be used to study the question posed, excepting where maternal effects (nongenetic effects associated with maternal parents and due to maternal half-sibs having a more uniform environment than progenies not so related) are present.

Maternal effects are probably not great in trees except where the trait is related to morphological and physiological factors of the seed. Thus, in the progeny data, germinability, speed of germination, and cotyledon number likely contain maternal effects and this is evidenced by the fact that the mother tree component for these was unusually large in comparison to error. The maternal effect in cotyledon number is due to the strong relation of this factor with seed weight. Seedling height and stem diameter possibly contain small maternal effects because of their relatively weak association with seed weight. The remaining progeny traits likely contain no maternal effects.

For the reasons discussed above only the progeny data of Table 8 should be considered in comparing within-stand vs. between stand variation. In the 10 traits of Table 8 the mother tree component of variance was usually not greatly different from the stand-within-group component. In four of the traits the mother tree component was much less than the group

component. Thus, even if one considers the varieties as separate taxonomic entities, genetic variation within stands was usually not much greater than stand-to-stand variation. The data suggest that genetic gains are feasible through selection among stands as well as among individuals within stands in slash pine.

Diversity Among Individuals Within Stands

The degree of variation among trees within stands is of interest in determining the genetic structure of the transition zone. If the two varieties are actually distinct and occur sympatrically within the transition zone, one would expect the variation among mother trees within stands to be greater in that area than elsewhere. This is so because mother trees were selected at random with no consideration of varietal differences (which, in any event, are not distinct in mature trees). If introgressive hybridization has occurred (recently enough to still be apparent) one would not only expect greater variation among mother trees but also among seedlings within progenies.

In order to study this problem, coefficients of variation (C's) were computed as outlined below:

- 1. In the parental data variances were computed among mother tree means within stands (5 or less per stand), for each trait, and C's were obtained from these (making 54 C's for each of 12 traits).
- 2. In the progeny data of Nursery Test 1, two kinds of C's were obtained:
- a. C's were computed among mother tree means within stands (5 or less per stand) as in "1" above (54 C's for each of 10 traits).
- b. Variances were computed among the five (or less) seedlings of each progeny (mother tree) and then pooled for each stand, and C's were computed therefrom. Thus, each C here was based upon 25 or less seedlings and there were 54 C's for each of 10 traits.

3. In the progeny data of Nursery Test 2, C's were computed among mother tree means as in "1" above (54 C's for each of 3 traits).

Pooled, within group averages of the C's outlined above were then obtained in order to compare the magnitude of diversity among elliottii, transition, and densa stands. Results are shown in Tables 9 (lower part), 10 (central and lower parts), and 11 (lower part).

Contrary to expectation, C's were not generally highest in the transition zone. In some cases the group averages differed little, while in others large differences occurred. In two of them, germinability and speed of germination (Table 11), average C's were high in elliottii stands and low in transition stands. But on the whole there was a tendency for these measures of variation to be highest in densa stands, intermediate in transition stands, and lowest in the elliottii stands. This is apparent in the following tabulation, showing the numbers of average C's for each group classified according to their relative magnitude. (For stomata per mm. of length in parental data, where groups 1 and 2 had equal averages, a value of 1/2 was entered in both "highest" and "intermediate" classes; a similar procedure was followed in other cases where group averages were equal.)

Group	Highest	Intermediate	Lowest
1	6-1/2	13-1/2	15
2	9	13	13
3	19-1/2	8-1/2	7
Totals	35	35	35

Table 9 .-- Coefficients of variation for parental data -- per cent

•	Cone	Cone diam- eter	Seeds per cone	Seed Nee: velght:per:	:Needles :: :per :: :fascicle:	Medle	Sheath length	: :Rows of :Stomate Weedle:Sheath:stomate :per mm. length:length:per mm. : of : of width:length	** ** **	Stomate: per mm.:Stomate: of :per : length :sq. mm.:	Resin: ducts:	Hypo- derm layers
					AMONG	STAIDS						
m	7.0	5.0	33.7	12.1	73.6	0.9	7.1	3.9	7.	2.6	8	2.2
CU (7.6	10.1	54.6	7.2	56.7	0.9	4.6	4	3.7	1.9	2, 2,) -4 -4
A11	15.1	8.6	51.9	27.3	57.6	8.6	15.0	3.5	0.4	5.7	0	70.00
groups	29.4	4.6	41.6	14.7	81.4	23.9	8.0	4.5	3.9	7.5	8.8	5.7
			2	OLED, AM	ED, AMONG MOTHER	TREES	MINHIN S	STANDS				
-10	12.4	88	37.9	18.8	109.8	88	800	4.8	9.9	10.5	15.5	3
3	12.6	8.8	43.7	19.0	161.2	7:1	7.5	8-5-	0.1	700	14.8	7.5.
groups	12.4	8.5	39.4	18.7	110.0	8.9	8.6	8.7	6.5	10.1	15.9	6.7

a Within entire species range (not pooled).

b Pooled, within groups.

Table 10. -- Coefficients of variation for progeny data of Mursery Test 1 -- per cent

Total height	Stem dism- etor	: Needles : per : fascicle		Needle length	Sheath length	stomata per mm.	per um. of	Stomsta per sq.	Resin ducts	Hypo- derm
					AMONG STANDS	NDS				
4	5.1	9 4		9.4	4.7	3.7	2,3	4.2	7.1	9.9
17.8	0.6	7.1		4.9	2	To Ch	3.0	5.5	5	0,0
39.1	9.5	क्र.		9.9	8.0	4	2.7	5.7	2.0	5.8
-	1	-		1	1	1	1		-	-
0° to	9.5	13.2		4.6	7.6	0.4	3.0	5.7	5.2	7.1
		P3	OLED,	AMONG 1	MOTHER TREES	KES WITHIN	STANDS			
10.9	8.8	1.6		6.3	0.6	9.9	4.3	7.5	10.2	9.5
15.2	8.3	15.4		7.2	6.1	7.0	T. 4	7.6	9.5	0
14.5	11.9	19.7		7.5	11.9	1.9	3.9	4.9	11.2	8
				,			1.	1		
groups 11.7	0.5	17.7		2.9	0,0	9.9	2.4	40-	10.2	9.5
		POOLEI	-	AMONG SI	SEEDLINGS	WITHIEN MOTHE	HER TREES			
0·18	16.0	19°4		17.4	15.5	10.7	8.2	12.7	17.9	16.0
24.5	17.5	4.08		13.9	13.5	12.4	8	14.9	17.2	16.5
28.9	800	36.4		13.3	20.0	13.2	8.6	15.6	18.9	16.8
-				1		1	-	-	-	-
groups 22.2	17.2	8, 12		13.0	17.0	11.2	8.6	13.4	18.1	16.1

a Within entire species range (not pooled).

b Pooled, within groups.

Table 11.--Coefficients of variation for progeny data of Nursery Test 2--per cent

Group	Germinability :	Speed of germination	: Cotyledons
	AMONG	STANDS	
1	16.0	17.6	4.6
2	23.6	13.7	7.2
3	18.1	10.6	7.2
ull groups ^a	18.5	19.4	6.0
PO	OLED, AMONG MOTHE	r trees within sta	AMDS
1	28.8	28.2	5.7
2	13.7	13.8	7.2
3	19.0	15.5	4.6
All groups b	25.3	23.7	5.8

a Within entire species range (not pooled).

b Pooled, within groups.

A chi-square test of independence was computed on the data of the above tabulation (Snedecor, 1956, p. 225). The null hypothesis of independence was rejected (P < .025). But since the average C's were not highest in the transition zone, the results present no evidence of recent hybridization or of the presence of a "mixture" of individuals of the two varieties in the transition zone.

In order to examine within-stand diversity more closely, the individual stand C's were plotted on maps as was done for trait values.

Diversity was frequently found to be lowest in the north-central region,
the coastal area of Georgia, and north-central Florida. It tended to be
high in south Florida, and moderately high in central Florida, the west,
and the northern fringe area. Speed of germination and germinability
were notable exceptions—as expected from the group averages discussed
earlier, their patterns were largely opposite to those shown for most
traits.

It is pertinent at this point to explore the possible causes of the patterns of diversity. The pattern shown by the bulk of the traits shall be considered first. One possibility lies in the existence of islands during the Pleistocene, many of which occurred in Florida. Presumably, many of the islands were very small at times, permitting fixation of genes by genetic drift. Migration following subsidence of the ocean level could then cause a mixing of different genotypes from different islands and from the mainland. This, however, would not explain why the coastal areas of Florida tended to show more diversity than those in the interior. Stands in the coastal areas must have resulted through migration from the interior islands or peninsulas

after each subsidence of the ocean level. Similarly, this gives no explanation for the moderately high diversity in the west and the northern fringe area.

Another possibility (not necessarily exclusive) is that high diversity was due to the presence of critical and highly fluctuating environmental factors. As noted earlier, the extremities of the species range are generally characterized by more severe climatic factors than interior portions. In some cases these factors are fluctuating or occur sporadically, such as the alternating drouth and flooding in the south (Langdon, 1958b), tropical storms in the south and coastal regions, and ice storms in the extreme north. Under such conditions the populations involved must maintain high diversity in order to survive. That is, they must maintain a variety of genotypes, some well suited to the extremes of the environmental factors and some to normal conditions. The diversity may be maintained by heterozygote preference (balanced polymorphism), as shown by Dobzhansky (1951, p. 117) in Drosophila populations. Under less critical and/or stable conditions, on the other hand, there is less need for maintaining highly divergent types, with natural selection favoring those most suited to the favorable or stable conditions.

Why did speed of germination and germinability show a trend opposite to that for most traits—the tendency for high C's in the north-central area and low ones elsewhere? A reasonable explanation is that strong natural selection for rapid germination has occurred in the south due to prevalence of adequate moisture in October and winter drouth. That is, the selection was probably strong enough to eliminate or greatly reduce the number of types that fail to germinate

promptly, ahead of the coming winter and early spring drouthy season, thus causing low variation in this trait. In the north-central area, on the other hand, maintenance of variability in respect to speed of germination may be most conducive to survival of the population. Here conditions favoring fall germination occur sporadically and there is probably a need for maintaining both dormant and nondormant types. Germinability may merely be related to speed of germination through pleiotropy, explaining why it tended to follow the pattern for speed of germination.

The hypothesis suggested by the results is consistent with commonly accepted theory of evolution and speciation in that species are so constituted as to attain a balance between fitness of individuals to the prevailing environment and heterogeneity, providing maximum likelihood of survival of the species as a whole in a changing environment (Dobzhansky, 1951, p. 108, and others). The heterogeneity is provided by mechanisms inherent in the species such as balanced polymorphism and others. It is only a step further to surmise that the magnitude of the heterogeneity will depend upon intensity of the factors causing it—the severity and degree of fluctuation of environmental conditions, and the nature of the trait (i.e., the degree of its adaptiveness) under consideration.

Although the explanations for diversity within stands seem logical, they are actually little more than guesses, further study being needed on this subject.

Diversity Among Stands

Thus far the degree of variation among individuals within stands has been considered. Another question of interest concerns differences in the degree of variation among stands within portions of the species range.

In order to examine this question, coefficients of variation were computed among stand means within the three groupings of stands already described. The data are shown in the upper parts of Tables 9, 10, and 11.

The results followed a pattern similar to that for variation within stands—C's were highest in densa stands, intermediate in transition stands, and lowest in elliottii stands. The pattern is seen more clearly in the following tabulation, showing the numbers of between-stand C's for each group classified according to their relative magnitude.

Group	Highest	Intermediate	Lowest
1.	4-1/2	6	14-1/2
2	7	10-1/2	7-1/2
3	13-1/2	8-1/2	3
Totals	25	25	25

A chi-square test of independence was computed on the above data and the null hypothesis of independence was rejected (P < .01).

What factors might have caused greater variation among stands in the south compared to the north? The fact that individuals within stands in the south were also more variable may have had some effect, since the variation in stand means depends partially upon variance among individuals. However, if the variation among stands was due entirely to variation among individuals, the differences between groups would have been

considerably less. For example, in that case, the stand C's would have been approximately $\frac{1}{5} = 0.45$ as great as the mother tree C's, because there were usually five mother trees per stand. Similarly, the stand C's would have been only $\frac{1}{25} = 0.2$ as great as the seedling C's because there were usually 25 seedlings per progeny. That this was not so is apparent in the data.

It is possible that differences in stand variation were due largely to the fact that sampling was less intensive, geographically, in the south than in the north—that is, on the average, stands sampled were furthest apart in the south. Another possibility lies in the existence of islands during the Pleistocene. As noted earlier, these occurred to a greater extent in central and south Florida than in the north. Effects of genetic drift, presuming they occurred, may have then persisted in some degree to the present time.

Still another possible explanation is that variation in soils and some climatic factors is greater in the south than in the north. Although concrete data on this comparison is lacking, Harper (1927) stresses the importance of high habitat variation in the ecology of the south. High habitat variation could, of course, cause high genetic diversity among stands through natural selection.

Multivariate Analysis

Table 12 gives D values obtained from the Mahalanobis' distance function analysis decribed earlier. Note that the tabulated data are the square roots of the distance functions, D², and that they were then multiplied by 10 to eliminate decimals without losing accuracy. The

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Table 12.--D values (x 10), with stands arranged in order of decreasing similarity to 8 stands in the north-central region

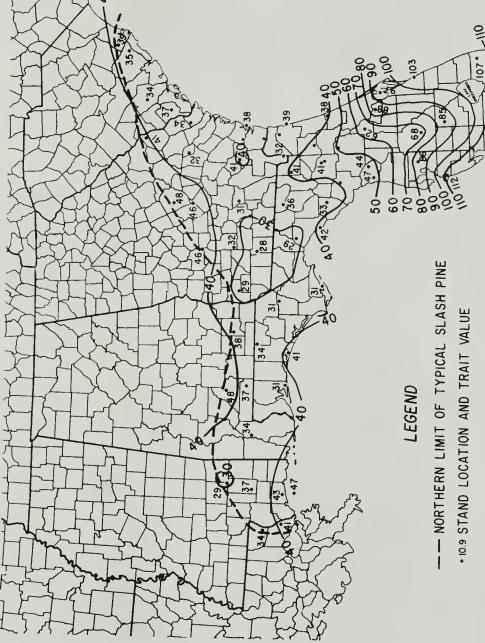
213 3123 21383 望なな83 323333 記れながはぬめ コメネジススペン なるおいれたなので 3はなななながななのな はいいだい はんない はんしょう \$8\$8992222EE 21232323233333 52528888855HB 22388738285528 NESSEE ERSEE **2002428834444888449** 8H433H4844458489333 3E3833328252525555555 **M33%%3%33%33%64%%26**8888 55555888368888888855588885545 M4333383933333535888888888888888 5888288248582485848855889B 2158828332788828882885832885558 11211003554867EF545483654838E3K 3E838884382E888EEEEE632E8888E RESERVATE STATE ST MW3248344834844233884484483388834388 53582828282882583865838623883288832866 \$3883883883875285555555773867888658586888 TEEPER SER BERRETER SER BERRARE BREEFER BREEFE

magnitude of each indicates the degree of similarity (not necessarily true relationship in the genetic sense) between the respective two stands, taking into account simultaneously the 17 traits used in the analysis. Thus, a relatively low D between two stands indicates a relatively high degree of similarity, while a high one indicates dissimilarity.

In general, the results agreed well with results of the single variate analyses. Examination of the D values immediately revealed that D's between stands in the north-central region and those in the south were greatest. In order to examine this point further a group of 8 stands (Nos. 14, 15, 16, 18, 19, 20, 24, and 34) within the northcentral region, which showed a very low within-group average D, were selected. Then the D value between each of the other stands and those eight were averaged to obtain a value indicative of the degree of similarity to stands in the north-central region. For example, for stand no. 1, the D values between stand no. 1 and the 8 selected northcentral stands were 39, 46, 40, 42, 47, 39, 38, and 35 (from Table 12); the average of these is approximately 41. Comparable averages for the eight north-central stands chosen were also obtained by computing average D values among them. For example, for stand no. 14, the D values between stand no. 14 and the other 7 north-central stands were 26, 29, 24, 26, 36, 30, and 34; the average of these is approximately 29.

The average D values, computed in this manner, are shown in Figure 33 (also, in Table 12 the stands are arranged according to the magnitude of these averages). Note that the data in Figure 33 revealed a familiar pattern, with a north-south clinal trend and a reversal in the north-

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of similarity to that region. Relatively low values indicate stands within the north-central region, showing the degree Figure 33. -- Averages of D values between each stand and eight similarity, while high ones indicate dissimilarity.

central region. The gradient is steep in central Florida. In the whole northern region an east-west pattern is also apparent--stands within the north-central region were more closely similar to each other than to those to the east or west.

It is important to note that Figure 33 expresses only the similarity of each stand to those in the north-central region. Thus, stands having roughly equal averages are not necessarily closely related to each other, although this is frequently true as will be seen later.

In order to exemine relationships among stands in various portions of the species range, the "cluster technique" described by Rao (1952) was used. The process began by first selecting pairs of adjacent stands which showed relatively small D values. These pairs formed the nuclei for clusters. Additional stands were added to each, the requirement for acceptance being that the proposed addition does not greatly increase the average D and that it fit better than in other clusters. In forming the clusters it was found that the average D usually increased with the addition of new stands, frequently because of the existence of clinal variation. Thus, the number of clusters formed was highly arbitrary. However, in view of the fact that the main purpose of clustering was to show relationships between clusters rather than to designate ecotypes, the procedure was considered satisfactory.

The result of the clustering process is shown in Table 13. A total of 10 clusters, containing from 1 to 10 stands each, were formed. Note that the within-cluster averages (the value on the extreme right of each row of values) is smaller than the between-cluster averages in each case, which shows the effectiveness of the clustering procedure. With a few

Table 13.--Average within- and between-cluster D values (x 10), clusters formed as described in text and arranged in order of decreasing similarity to "North-central (west)" clustera

Cluster	:Stand : (n) :	:Stands:cen-:cen-:(n):tral:(west):(esst)	cen- :cen- :tral :tral :(west):(esst)	West-:		North-: North: ern east-: Fla.: (Coar ern : al	North: ern : Fla. : (Coast-: : al) :	North- ern fringe	Cen-: tral: Fla.:	South : Fla.	Fla. Keys
	Manber	i i	1	1	Av	Average D (x 10)	(x 10)				1
North-central (west)	8 (30									
North-central (east)	4 (ਲੈ	8								
Western	9	36	36	8							
Northeastern	9	38	35	35	33						
North Florida	10	147	39	147	39	ਨੈ					
Western (coastal)	8	#	24	04	98	24	33				
Northern fringe	77	45	94	41	36	42	35	30			
Central Florida	5	111	11	73	Z.	62	22	70	17		
South Florida	9	109	105	101	103	8	107	100	63	84	
Florida Keys	Н	911	911	106	109	112	211	108	8	19	;

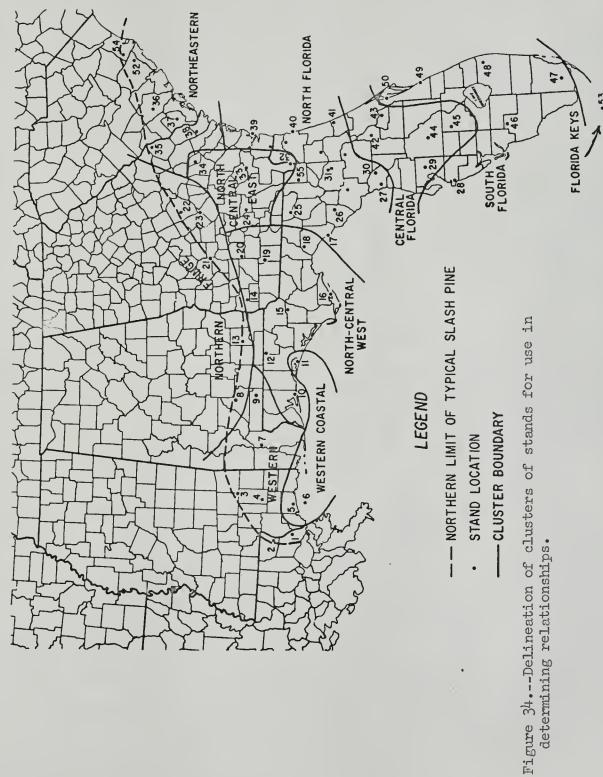
a The number of D values upon which each of the between-cluster averages is based is equal to the product of the two respective "n's"; for within-cluster averages the basis is (n) (n-1)

exceptions, the stands within clusters are contiguous geographically (Fig. 34). One of the exceptions is the "Western (coastal)" cluster-stand 11, curiously, is widely separated from 5 and 6. The fact that stand 14 fitted better with the "North-central (west)" group rather than with the "Northern fringe" was also puzzling.

The relatively large within-cluster averages for "Central Florida" and "South Florida" are apparently a consequence of high stand-to-stand variation noted earlier in the single-variate analyses.

The approximate degree of similarity among clusters is shown in Figure 35, which is based upon the data of Table 13. Note that the figure does not show all possible D values and is not drawn to scale accurately—an impossibility with only two dimensions. Nevertheless, clusters appearing close together in the figure are relatively similar, while those far apart are dissimilar. As can be seen, clusters near to each other geographically tend to be relatively similar, largely because of clinal trends. However, note several exceptions. For example, "Northern fringe" is more similar to "Central Florida" (average D between these two clusters = 70) than is "North-central (west)" (average D between "Central Florida" and "North-central (west)" = 77), even though "Northern fringe" is furthest from "Central Florida" geographically. The same situation is true for the "Northeast" cluster. This seemingly anomalous situation is apparently a consequence of the trend reversals commonly occurring in the north-central region, pointed out earlier.

The "Western (coastal)" and "Northern fringe" clusters curiously hang together and the reason for this is obscure. The "North Florida" cluster is more similar to those in the south than are clusters in the north, as might be expected because of the clinal trends.



determining relationships.

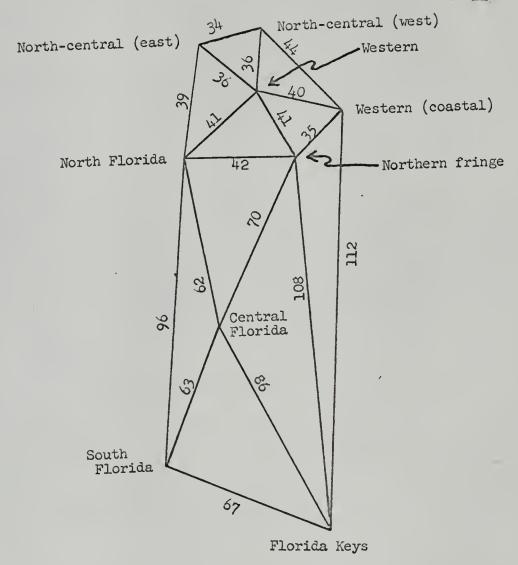


Figure 35.--Diagrammatic representation of the approximate degree of similarity among clusters of stands according to average between-cluster D values. "Northeastern" cluster, not shown above, is very similar to "Western." For average D values not shown above, see Table 13.

A test for clinal vs. ecotypic variation was made by a procedure similar to that discussed by Wells (1962) and Wright and Bull (1963). A transect extending from stand 24 in the north-central region southward through the approximate center of Florida to stand 47 was delineated. D values between the stands represented on this transect are compiled in Table 14. Note that D values for geographically contiguous stands (those on the extreme right) are smaller than those to the left (noncontiguous stands), and that they generally increase from right to left within a row or from top to bottom within a column. This shows that contiguous stands are more similar to each other than noncontiguous ones, and that the further two stands are apart geographically the greater is their dissimilarity. The values change relatively more rapidly near the center of the transect than they do at the ends. This is a consequence of the relatively steep gradient in trait values in central Florida, shown earlier, for a number of individual traits. The change in the rate of change in central Florida, however, hardly justifies delineation of ecotypes as the variation is largely clinal to the north, to the south, and across, the central area.

Two other transects were formed--one extending from the north-central region southward along the east coast of Florida and the other beginning in the same region and extending southward along the west coast of Florida.

The results in both cases were similar to those of Table 14.

In the above analysis, stands in the north-central region were used as starting points to test for latitudinal clines. The reason for this was that above this area the trends change direction, as shown in Figure 33, and in many of the individual trait patterns. Because of the limited

Table 14.--D values (x 10) for stands in a transect going from stand 24 (north-central region) southward through the center of Florida to stand 47 (south Florida).

Stand	54	55	31	42	144	45	46	:	47
5/1									
55	29								
31	30	27							
42	56	47	37						
111	64	62	55	46					
45	82	76	64	51	40				
46	114	110	100	84	70	56			
47	119	114	103	86	68	67	53		

breadth of the northern fringe area it is difficult to prove a clinal trend with the use of D values but there is little question that it exists. Observation of Figure 33 and many trait patterns shows that changes northward from the north-central area are usually gradual.

The D values show no evidence of an unchanging longitudinal cline in the north. This, however, does not mean that racial variation does not exist in the north, nor does it mean that changes are not gradual. The study of clusters, as well as the individual trait patterns, showed that longitudinal variation does occur in the north. The pattern, however, is not a simple cline. The clusters delineated in the north could be considered as ecotypes, but with the qualification that changes between ecotypes are gradual. Another way to describe it might be to say that the longitudinal variation is continuous but highly fluctuating.

Nomenclatural Considerations

In view of the fact that most of the traits studied showed continuous variation, one may question the division of the species into varieties.

The differences between slash pines in the north and those at the extremes of the species range certainly are striking in several respects and they are genetic to a large extent. It seems proper therefore to ascribe different names to these extreme types. The common name "South Florida slash pine," and even its scientific name, have become well accepted and the separation certainly serves a purpose. It is better, for example, to prescribe silvicultural treatments separately for the two varieties than to prescribe a single treatment for the whole species, or to label seed as being of one or the other variety rather than to label it merely "slash pine."

However, there are those who feel that subdivision in the presence of clinal variation is misleading and does more harm than good, because it gives a false impression of homogeneity within the taxonomic subgroups, disguises gradients among subgroups, and discourages study of variation among subgroups (Hurley, 1938; and Langlet, 1959 and 1963). This viewpoint certainly has merit. Subdivision also tends to impart a certain degree of "smugness," causing laxity among both forest managers and researchers. It becomes tempting, for example, to assume that trees at the extreme southern tip of Florida would require exactly the same silvicultural treatment as those in central Florida because they are both South Florida slash pine, while trees just beyond the "boundary line" require a different treatment because they are of a different "species" (many foresters have actually elevated the subdivision to a species level in their thinking and conversation).

Irrespective of nomenclature, one should keep in mind that South

Florida slash pine and typical slash pine may not be discrete genetic

entities cleanly separated from each other morphologically, physiologically,

or geographically; that many traits show clinal variation both within and

between the varieties; and that for some purposes, especially (but not

limited to) seed collection, it is therefore highly desirable to specify

the exact geographic origin of material rather than merely specifying its

varietal name.

SUMMARY AND CONCLUSIONS

The main purpose of this study was to determine patterns of geographic variation for a number of morphological and physiological traits of cones, seeds, foliage, and seedlings in slash pine, and to determine the causes of such variation where found.

Mature comes and foliage samples were collected from each of 5 trees in 54 natural stands scattered throughout the species range in the fall of 1960. Seeds extracted from the comes were sown in a nursery at Olustee, Florida, in the spring of the following year, and foliage samples were collected from the resulting seedlings in the fall of 1961.

Data were taken on 12 traits in the parents and 13 traits in the progenies, and were subjected to analyses of variance to determine the proportions of variance associated with groups of stands, stands within groups, and mother trees within stands. The parental data gave information on phenotypic variation associated with locality while the progeny data, for the most part, gave information on the extent of genetic variation associated with locality of source. Isograms were drawn to elucidate patterns of variation where justified. Regression analyses were employed to study relations with climatic factors. A distance function was used to study a group of traits simultaneously.

Major findings and conclusions follow.

1. Most of the traits studied showed significant differences associated with the geographic source of the material. In the parental data such stand-to-stand variation was relatively strong for cone dimensions, seed yield per cone, seed weight, needles per fascicle, needle length, fascicle sheath length, and hypoderm thickness, while it was relatively weak or absent for various measures of stomatal frequency and frequency of resin ducts. In the progeny data, stand variation was strong for total

120

height, stem diameter, needles per fascicle, needle length, germinability, speed of germination, and cotyledon number, while it was relatively weak for sheath length, stomatal frequency, resin duct frequency, and hypoderm thickness.

- 2. Most traits showed some type of clinal or continuous variation, containing one or more trend reversals. The clinal patterns apparently resulted from genetic adaptation to gradients in environmental factors. The trend reversals were probably due to the existence and interaction of two or more factors affecting each trait. Random variation, possibly due to genetic drift, was found in a few instances.
- 3. Many traits showed a generally north-south trend through Georgia and Florida with a reversal in the north-central region (extreme south Georgia and north Florida). This general pattern probably resulted from the latutudinal gradient in winter temperatures (or similar factors) and in seasonal distribution of rainfall. Curvilinearity or interactions of these could be the cause of the reversal.
- 4. Longitudinal variation also existed in the north but was usually not as pronounced as latitudinal variation. The longitudinal pattern for most traits could be described as being continuous but highly fluctuating.
- 5. Multivariate analysis similarly revealed a latitudinal gradient through Florida and Georgia, which contained a reversal in the north-central region and which was relatively steep in central Florida. Thus, stands in the north-central region were less similar to those in south Florida than were those in other portions of the north.
- 6. Variation among trees within stands tended to be least within the north-central region, the coastal area of Georgia, and north-central Florida, and greatest in south Florida and other extremities of the species range. This was believed to be due to the existence of severe environmental factors in the latter group, which probably fluctuate greatly in time, resulting in maintenance of a greater variety of genotypes than in the central areas.
- 7. Variation among stands tended to be low in the north and high in the south. This may have been partly due to prevalence of islands in Florida during Pleistocene times, causing stand variation through genetic drift, and possibly to higher variation among habitats in the south than in the north.
- 8. Trees growing within the ranges of the two varieties showed dissimilarity in several respects, but patterns were usually continuous both within and between varieties. No evidence of the existence of two distinct types (representative of varieties) was found within the transition zone. Likewise, no evidence was found to suggest that trees in the transition zone are hybrids between densa and elliottii varieties. Hybridization and introgression may have occurred during the Pleistceene or earlier but if so, subsequent natural selection has apparently obscured it.

These conclusions were based largely on the fact that diversity among trees within stands was not greatest in the transition area.

9. The sampling design used, although much more intensive than that employed in past slash pine studies, contained several deficiencies. A greater intensity of sampling in central and south Florida would have given a better measure of differences in stand-to-stand variation in different areas. More mother trees per stand and more progenies per mother tree would have given a better measure of variation within stands, an important consideration in studies of this nature. Finally, it may have been preferable to delineate zones for sampling purposes and select samples randomly within zones. These and other deficiencies of the study should be considered in evaluating its results.

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APPENDIX

KEY TO APPENDIX TABLE 1

Column no.	<u> Item</u>
1	Mother tree identification. The first digit indicates group number; the second and third, stand number; and the fourth, mother tree number.
2	Sum of the lengths of seven conesinches. Decimal between second and third digits.
3	Sum of the diameters of seven conesinches. Decimal between second and third digits.
4	Average number of seeds per cone.
5	Number of seeds weighed.
6	Total weight of seeds indicated in column 5milligrams. Column 6 divided by column 5 gives average seed weight.
7	Number of ternate fascicles in a sample of 40 fascicles.
8	Sum of the lengths of 15 fasciclesmillimeters.
9	Sum of the lengths of 15 fascicle sheathsmillimeters.
10	Sum of the numbers of rows of stomata on the flat surface (or surfaces) of five needles.
11	Sum of the flat surface widths of five needlesmicrometer units. (100 micrometer units = 1.68 mm.) Col. 10 x 1 = number of rows of stomata per mm. of needle width.
12	Sum of the numbers of stomata counted in 10 stomatal rows, each 1.68 mm. long. These values, divided by 16.8, give numbers of stomata per mm. Also, Col. 10 x Col. 12 x 1 = number of stomata per col. 11
13	Sum of the numbers of resin ducts counted in each of five needles.
14	Sum of the numbers of hypoderm layers counted at four points in each of five needles. These values, divided by 20, give average numbers of layers of hypoderm per needle.

1	2	3 .	_ 4	5	6	7	8	9	10	11	12	13	14	
1.6.1.1		2.1.	1.05	1.2	7505		2720	0.7						
1011	290 273	112			4595		2739				17/	36	41	
1012 1013	278				3056 3342			240			132	30	41	
1014					4062		3102			441	174	34	42	
1015	384				4177		3433	295	53 48	449 496	168	32	47	
1021	311	121	081		3697		2800	265		424	198	40 37	43	
1022		132			3534		3495	276		474	170	25	49	
1023					4117		3297	301	51	493	18)	20	43	
1024	289				2866		3137	245	46	419	163	26	43	
1025	306				3318			260		499	191	2٤	41	
1031	262				3054		3023	183			181	15	41	
1032	364	113			3349		3203	288			181	27	40	
1033		111	041		3954		2910	236		441	156	33	41	
1034	296		050		3641			214			181	34	41	
1035	320	131			5811				58		170	37	43	
1041	369		085		5154		3175		61		172	37	43	
1042	334	122	057		4687		3367		44	451	179	27	49	
1043	269	116	070	132	3526	002	2998	264	42	445	190	35	42	
1044	355	127			3545		3267		62		193	33	41	
1045	285	113	047	132	2853		3126				174	31	43	
1051	358	140	059	132	3379	25.	3305	ر 28	54	471	161	26	44	
1052	427	134	031	132	4558	30.	3713	31.	54	495	167	23	42	
1053	269	116	032	132	2921	12.	3491	304	51	465	150	43	47	
1054	249	110	064	132	3341	01:	3630	248	50	445	166	35	44	
1055	319	134			3705	04.	3207	222	44	391	186	26	41	
1061	305	105	040	132	3079	152	2998	249	41	427	172	21	46	
1062	320	102	026	132	3719	002	2884	241	6 i	47.	174	43	46	
1063	280	122	015		3652		2690	254	40	451	183	43	47	
1064	234	11.	020		3095		2508	224	53	45)	172	34	46	
1065		035	046		2597		2857	230	50	45%	161	40	46	
1071	225				4036_		2891	260	50	440	155_	40	41	
1072	269		041		3493		3277	230	52	435	17)	3 3	43	
1073		122			3239		3115		54	521		35	42	
1074					4155		3184				190	29	40	
1075					4213								40	
1091					5135						16	37	40	
1082					3824						175	39	40	
1083					6098						170		41	
1084					4584						194 150		41	
1085					4627			252				37		
1091					4078 3895						17/	25 32	4 U	
1093					4532						184	36	42	
1095					3727						190	41	44	
1101					5151			290			163	33	41	
1102					4596			305			169	50	45	
1103					3540			-			185	38	42	
1104					3451					466		24	40	
			0.0	W -7 L										

						σ Δ	_	7.0	2.7	3.0	7.0	7.7
	2			5		7 8			11		13	14
1105		10,1		1324		023372	266	58	473	175	41	40
1111	322	122	038	1324		183282	297	55	431	159	_26	42
1112	298	109	043	1323		253260	260	48	431	165	31	40
1113	365	133	065	1325		263066	266	52	472	164	27	41
1114	356 350	131	038	1324		063386	279	54	466	155	38	44
1115	289	110	017 065	1323 1324		003336 113529	272	55 40	440 ₂ 392	182_	_34 _27	43
1122	365	115		1324		273604	256 314	51	467	171 169	28	42 39
1123	242	117	073	1323		353515	309	55	488	161	35	43
1124		096		1324		153497	313	55	484	164	40	39
1125		133	099	1324		083518	312	48	448	187	36	46
1131		118		1324		013205	221	40	409	160	23	41
1132		146		1326		003309	237	44	370	167	21	43
1133		120	033	1324		003111	231	46	446	163	33	38
1134	327	116	046	1324		033201	210	50	452	189	30	44
1135	283	116	062	1324	082	033440	267	43	397	174	28	3+
1141	232	104	039	1323	970	243556	234	50	457	156	22	43
1142	274	106	_063	1324	647	013299	311	45	405	179	31	43
1143		114		1323		022881	294	51	471	196	34	41
1144		111		1323		123798	293	52	475	155	40	43
1145		110	073	1324		053643	316	61	453	151	42	39
1151		104		1343		13405	313	60	426	149	34	40
1152		129		1325		013396	272	52	466	173	35	42
1153	371		085	1323		113568	341	38	431	171	34	44
1154		103	063	1324		403127	296	51	480	172	36	43
1155 1161		100_	027_	1323		013616	323	41	444	183_	_34	42
1162	317	111	060	1323 1324		013533	267	62	495	162	40	40
1163	279	091	083	1323		113479	321 254	55 46	432	173 172	<u>42</u> 32	40
1164	246		063	1323		002556	25°	42	426	185	35	45
1165	312			1324		033518	305	60	497	175	36	40
1171	298	107		1324		263501	280	58	492	146	35	39
1172	305	097		1322		143353	294	56	507	150°	34	40
1173				1325		403647			557		30	44
1174				1323		023330			472		32	47
1175				1323		032930	250		437		34	37
1181	405	125	010	1325	628	013606	284	54	437	185	36	43
1182				1324	104	023220	290	52	459	184	40	41
1183		101		1324		003353		61	487	185	41	41
1184				1324		053202			431		40	39
1185				1324		063190			422		31	39
1191				1324		103455			469		_33	43
1192				1323		003480			504		42	40
1193 1194				1325		233688			550		_30	39
1195				1323 1323		113408			465		40	42
1201				1325		273101 003573			540		39	38
1202_				1323		243127			445 460		37 36	43 38
1203				1322		022796			473		37	39
1204				1323		022808			472		39	41

1	2	_3_	4	5 6	7 8	9	10	11	12	13	14
1205	25,5	104	062	1325428	083374	264	57	535	180	32	40
1211	303	130					65	490	168	43	44
1212	359		045	1324423	013294	290	55	474	15+	34	44
1213	384	130	030	1324128	343202		61	523	161	37	40
1215	319	132	019	1224927	023240	279	58	488	181	35	41
1221	324	138	041	1325563	023231	275	56	458	162	33	40
1222	325	136	040	1324522	022876	255	48	439	159	24	38
1223	298	The Person Control of the Person of the Pers		1323998	013322	276	54	476	170	33	40
1224	328	140		1324105	013045	263		420	181	33	45
1225	284	117		0050130	403157	276	5 ວ	534	172	35	40
1231	243	105	006	0922902	303598	272	58	520	155	39	39
1232	268	110	006	0752196	003371	253	55	477	167	30	40
1233	276	120	008	1264211	073261	243	68	475	175	45	43
1234	267	108	030	1324175	0/3239	284	54	470	184	35	40
1235	311	123	006	08/3210	123586	270	46	445		23	42
1241	323	123	096	1325969	003060	273	51	481	190	33	39
1242	354	122	103	1323680	103472	270	53	435	166	38	40
1243	347	120	017	1103109	112942	280	69	547	182	51	42
1244	277	09)	061	1323115	103315	276	53	459	172	38	42
1245	300	106	042	1323067	002316	251	40	439	165	30	41
1251	370	104	087	1324065	193343	310	56	556	177	30	41
1252	308	111	021	1323134	012492	284	56	484	166	34	40
1253		120		1325145	213537	319	55	510	152	39	39
1254	277	09)	009	0320533	303161	300	60	523	172	25	43
1255	339	-		1324607	052720	244	48	484	160	28	44
1261	301	11)	057	1325758	342947	277	64	505	181	36	39
1262	366	136		1325304	403868	320	64	540	169	36	39
1263	367			1324699	223236	301	58	536	189	36	40
1264	312		026	1325061	003889	28 L	51	518	177	38	42
1265	309	100		1322862	023216	301		472		29	43
1311	340			1324924	103478	280		459		30_	41
1312	419			1325261	123533	270	49	514	181	34	42
1313	320			1323687	173697			483		29	35
1314	281	10)		1323911	043545	314	51	457		3 i	38
1315				1322494						35	43
1321				1324555				509		41	44
1322				1322957					183	33	41 -
1323				1324742					170	36	43
1324			_	1323764					186	38	41
1325				1323958					177	40	40
1331				1322600					184	_34 -	41
1332				1322608				510		34	41
1333				0210536				409		36	42
1334				1323123				431		30	40
1335				1322548	063289			425		31	40
1341				1322924				492		40 42	37
ــــــ1 42 1 343			-	1323497				508	man.	47	41
								479		39	40
1344	3/4	115	009	1323399	173157	200	20	419	154	24	40

Appendix Table 1 continued

,	_	_	,	r /	77 0	_	20	2.2	20	10	2.4
1	2	_3_	4	5 6	7 8	_9_	10	11		13	14
1345		IU,/		1323447	25/3444	295	63	511	155	36	41
1351	317	124	054	1324094		242	53	467	186	34	40
1352	279	114	047	1324137	003599	300	5 Ú	484	174	43	41
1353	299	126	031	1325771	033737		48	453	182	37	45
1354	273	101	040	1323990	203612	25 s	53	491	161	29	41
1355	314	127	044	1324663	013992	261	59	494	162	39	4()
1351	185	124	063	1323850	003340	246	50	436	177	30	40
1363	303	130	047	1324551	063509	311	52	473	171	25	38
1364	235	106	032	1322738	222932	235	55	488	167	32	4()
1365	306	123	042	1324965	213404	266	44	495	161	29	41
1371	271	123	034	1323693	203028	279	56	476	159	31	39
1372	315	125	077	1323721	003429	266	47	401	146	38	39
1373	257	113	040	1324429	003110	251	43	417	178	30	46
1374	323	120	030	1323915	283226		45	426	149	28	38
1375	314	127		1324316	2/2993		51	503		24	3.8
1381	284			1324853	083376				162	39	40
1382	303	115	046	1323755	002806				164	38	41
1383	321	123	060	1324670	103441		55	510	170	35	43
1384				1323067		190	54	504	178	39	40
1385			018	1322288	022/90		49	442	173	28	46
1391				1325534	373712			526	165	38	41
1392		122		1325257		271	72	561	15)	35	39
1393	388			1325404		245	68	541	183	39	41
1394			091	1325171	303575		55	486	163	39	44
1395		119		1324794	0+3705	291	60	537	175	40	44
1401	399	135	055	1326333	003717		67	50a	184	41	33
1402		11)		1325450	393388		61	533	184	34	40
1403			037	1324232		261	60	468	186	39	42
1404	340	112		1324352	153678		47	501	163	36	39
1405	286		034	1324615	044040	311	54		163	37	
1521			070	1324653		314	55	45/	155	35	41
1522	~	123	_	1324797	013686	-	55	531	189	38	42
1523			037	1323904	003147			446	180	37	43
1524		115		1323484	033532		55	469	15)	31	37
1525				1322580	003005			482		33	46
1541				1324037	183130			520	160		
1542				1322475	013402					28	40
1543				1322605	013029			500		43	40 =
1544				1323920				460		38	41
1545				1323532	023049			507		30	40
_ 1551				1324648	022981			51)		36	41
1552					003399		61		167	28	40
1553				1324468 1324863	133440				193	43	39
1554		A.M. J.			303182	-		551		33	40
1555				1324813	023969				169	44	41
2291				1324405	273577			510		31	40
2292				0210521	013145				173	21	42
				0671259	013369_			469		35	40
2293	215	104	003	0150535	043466	213	51	457	167	41	41

	2	_3_	1	5 6	7 8	9		_11_		13	14	
2294	256	103		070'2811	01'3872	279	46	427	171	35	41	
2301	276			1324539	152944		5 8	459	179	27	39	
 2302	328				113256			411	å81_	28	39	
2303	241	107		1324755	383368	261	50	495	163	37	40	
2304	299	110		_1324129	383141	275	_56	517	187	3.3	43	
2305	340	119		1324720	362893			464	180	28	43	
 2411	_333		- Angelon	1323909	293443		52		172	27	45	
2412		122		1323337	143485	356	61		180	47	43	
 2413		11/		1323507	073391	295	51		185	42	41	
2414		124		1323128	033448	287	49		176	33	42	
 2415		117		1324751	003572		46	499	201	30	54	
2421		137		1094282	364268	280	57		170	42	41	
 2422				1323283	093643	283_	51	451	165	_36	39	
2423		141		1323802	193240	320	61	546	206	39	46	
 2424		112	~	1323558	283821	270	56	510	194	25	39	
2425		114	016	1324477	053805	276	48	451	192	28	35	
 2441		105	045	1323786	013399	247	44	453	173	_ 35	44	
2442		091		0822118	023746	252	54	464	175	38	40	
 2443 2444		095	-	1323655	053676	194_	39	454	183	_31_	52	
2445		115	012	10,3729	372930	280	54		195	29	39	
 2451		103	049	0481460	133863		47		181	23	46	
2452	255	113	010	1142078	043096	237	46	416	183	28	39	
 2453	260	110	027	1323638	383205		48		165	24_	44	
2454		122	028	1324618	103933	250	59	523	163	40	40	
 2455		130	054	1324361	253143	265	59	519	200	31	45	
3271	259	122	040	1323441	343331	247	53	508	187	39	49	
 3272	333	130		1326377	034089			476	178	33	38	
3273		113	032	1324980	033891	291	57	510	184	42	43	٠
 3274		101	028	1326771	003236			449	177	40	41	
3275		117		1323862	033254	283	49	446	185	41	43	
 3281		102		1323127	153405	258	48	436	195	35	41	
3282		121		1323881	003194		43	480	18.)	32	48	
 3283				1325043	003965	330		502	182	38	42	
3284				1323866				561 474	166	47	41	
 3285				1324140	013690					33	44	
3431				1324812	053935			484 521	177	30	44	
 3432				1323498	033860		48 55		176	46	47	
3433				1323912	003453				200	34	42	
 3434				1324396	102956				189	<u>3</u> 8	43	
3435				1324609	004133		53	467		35	39	
3461				1323663	024237		57	527		39	42	
3462				1324635	003846		58	524		37	50	
3463				1324026	003846			516		41	54	
3464				1325066	004611		50	505		33	45	
3465				1324818	004335		55		174	44	45	
3471				1322641	063658				164	21	4.5	
3472				0991969	014383			381		30	3.)	
								-				

	2	_3	4	5 6	7 8	_9_	10	_11	12	13	14	
3473	285	109 (006	1084/201	4 00/3550	223	51	471	155	27	43	
3474	275	114 (010	0982261		194	39	432	147	24	51	
3475	227 1	119 (013	0721605	033721	204	51	481	182	31	47	
3484	201	110 (018	1323420	0 003867	255	56	520	173	41	51	
3485	293	114 (035	132422			58	494	175	37	50	
3491	248 (092 (010	1324029			56	454	168	-34 -37	43	
3492	268 1	105 (064	1323770			46	509	185	37	58	
3493	295]	116 (029	1325009			60	526	184	36	44	
3494	262 1	106 (38	1323332			58	491	180	35	41	
3495	300 1	100	174	1322927			50	509	192	35	55	
3501	366 1	15 (056	1324940		288	46	444	195	- 43 -	43	
3502	251 1	19 0	77	1324140		300	49	457	165	43	45	
3503	289 1	0/0	056	1323396		273	52	483	182	22	43	
3504	344 1	09 0	71	1323364		332	60	491	167	43	47	
3505	270 1	.05 0)57	1323507		285	57	548	183	31	54	
3531	193 0	75 C	002	0140134		169	51	498	157	34	51	
3532	215 1	.02 0		1011331		221	44	479	184	31		
3533	244 0			0190301		275	60	545	187	42	47	
3534	207 1			0170284		211	52	533	176	39	48 47	
3535 .	210 0	83 0		0720778		195		$\frac{272}{519}$	190			
					003110	2,7	1	フレノ	130	29	44	

KEY TO APPENDIX TABLE 2

Column no.	<u> Item</u>
1	Seedling identification. The first digit indicates group number; the second and third, stand number; the fourth, mother tree number; and the fifth, seedling number.
2	Total height of seedlingcentimeters.
3	Stem diameter of seedlingmillimeters.
4	Data not pertinent to the study.
5	Number of ternate fascicles in a sample of 10 fascicles.
6	Sum of the lengths of three fasciclesmillimeters.
7	Sum of the lengths of three fascicle sheathsmillimeters.
8	Sum of the numbers of rows of stomata on the flat surface (or surfaces) of two needles.
9	Sum of the flat surface widths of two needlesmicrometer units. (100 micrometer units = 1.68 mm.) $\frac{\text{Col. 8}}{\text{Col. 9}} \times \frac{1}{.0168} = \text{number of rows of stomata per mm.}$ of needle width.
10 .	Sum of the numbers of stomata counted in four stomatal rows, each 1.68 mm. long. These values, divided by 6.72 give numbers of stomata per mm. Also, $\frac{\text{Col. 8 x Col. 10}}{\text{Col. 9}} \times \frac{1}{\text{.04(1.68}^2)} = \text{number of stomata}$ per sq. mm.
11	Sum of the numbers of resin ducts counted in each of two needles.
12	Sum of the numbers of hypoderm layers counted at four points in each of two needles. These values, divided by 8, give average numbers of layers of hypoderm per needle.

Appendix Table 2.--Progeny data of Nursery Test 1

	•			-	-							
1_	2	3	4	5	6_	7	8	9	10	11	12	
10111	24	0808550	2700549	05	422	30	14	142	63	05	11	
10112	25		1906384	07	414	19	14	152	64	05	10	
10113	23		170/429	10	414	18	15	152	58	04	08	
10114	24	0711000	3250649	10	503	20	14	148	72	04	09	
10115	29	0807450	2800674	03	445	25	12	133	64	00	11	
10121	21	0604500	1550323	09	430	30	manus -	143	71	05	10	
10122	21	0705950	1900348	03	411	26	09	123	65	04	11	
10123	30	0807150	3250583		464	17	12	133_	66	04	12	
10124	29		01800298	80	413	21	13	130	66	04	10	
10125	31		1900368		345	22	15	145	67	04	12	
10131	18		01700390	IC	307	17	15	147	54	04	13	
10132	2.8		02106424	07	46C	28	17	172	59	05	11	
10133	21		01590374	10	530	23	18	164	60	06	10	
10134	23		02500543	_08	462	23	15	166	60	04	15	
10135	33		04210779	10	514	21	14	173	60	05	14	
10141	34		03266597	0.8	387	23	14	165	62	05	11	
10142	25		01750482	10	372	20	18	171	69	06	14	
10143	26		0335(612	_ 08	399_	24	16.	161_	61	04	15	
10144	25		11500527	0.9	419	21	15	149	63	04	11	
10145	19		01200332	0.5	425	_20	12	147	66	05	11	
10151	36		05280794	10	536	22	13	166	70	04	11	
10152	20		01660169	09	412	18	13	145	65 59	04	11	
10153	32		02700584	09	381	25	14	149		04	11	
10154	33		02930548	10	416	28	14	145	63	05	14	
10155	36		05341141	10	531	22		148	70	05	13	
10211	19		01700372	06	374	$-\frac{20}{20}$	16	136	64	04	09	
10212	19		01236307	07	417 456	20 21	13	138	64	04	11	
10213	26		0200(447	10	439	27	16	170	65	05	14	
10214	26		02000299	07	462	18	13	144	71	06	10	
10215	18 30		025005799	- 08	440	25	17	161	59	06	16	
10221 10222	23		03450783	06	441	26	16	142	58	04	13	
10223	28		0435(550	10	573	19	17		52	05	12	
10224	25		02105426	08	429	24	17	156	60	05	11	
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Appendix Table 2 continued								
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34345	08	07041201680581	07	421	16	13	146	65	06	11	
34351	09	07050701650509	04	418	25	09	121	52	04	12	
34352	10	06050001700629	05	545	23	13	120	58	04	10	
34353	16	09066004591005	01	600	25	14	122	57	04	12	-
34354	14	10109004800944	80	538	22	13	141	55	04	10	
34355	10	07064001820599	06	642	32	16	150	64	06	13	
34611	11	12067103840741	07	500	19	16	152	65	05	08	
34612	11	11063103590959	05	634	28	ló	162	53	05	14	
34613	10	10064703380753	10	470	22	14	145	60	05	10	
34614	13	11073003691038	03	569	26	14	149	66	04	80	
34615	12	10058902930882	10	678	30	16	153	51	05	09	
34621	13	10068004401012	10	543	30	14	140	59	04	11	
34622	10	11068604190761	06	693	26	20	159	62	04	14	
34623	15	10064903630670	10	766	31	12	134	54	04	09	
34624	12	_11068404540830_	10	707	30	12	149	59	05	14	
34625	11	07029301430394	06	395	28	16	181	51	07	15	
34631	13	11075004410867	06	554	24	14	128	6 L	05	12	
34632	12	09036302150605	09	615	31	14	155	67	80	15	
34633	16	10072504120636	10	652	23	12	126	52	04	13	
34635	11	07067301930513	10	627	24	15	151	55	04	10	
34641	12	10090203361058	05	570	34	12	138	60	04	15	
34642	11	15089004190788	03	575	24	12	122	62	04	12	
34643	12	08061903110877	05	633	25_	09	111	62	04	12	
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34711	09	09059002600618		459	19		110	59	04	80	
34712	10	11059502500573		587	21		102	59	04	09	
34713	08	07045501400363	09		22		129	62	06	11	
34714	_ 0 შ	10058502050553	08	542	25		121	_65_	05	09	
34715	09	08076502450603		521	16	11	112	56	06	10	
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34722	09	09079202260594		533	17		142	51	04	11	
34723	10	07042602210611		675	18		129	61	05	11	
34724	17	13066105071113		687	1 g		142	64	04 04	12 09	
34725	15	08093003400868		668	27		136	54 55	04	10	
34731	12	10061803120666		572 555	21		120 114	- 55 - 62	04 06	11	
34732	07	07025100950130		445	22		105	47	04	11	
34733	08	07034101300428		601	29		120	56	06	12	
34734	09	07043101350278 06044900920411	01	364	15		112	67	04	13	
34735	06	11074103190912		499	20		115	63	04	08	
34741	10	11074103190912	-02	477	20	12	117	0.5		00	

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34744	10	09082002880734	01 507	10	12 118	58	04	12
34745	11	09090903810720	02 577	28	11 122	56	05	11
34751	09	12048803000620	08 532	17	12 129	60	04	09
34752	80	_09042501500310_	07 564	_21	12 130	58	04	10
34753	16	11092002950639	07 638	33	12 146	61	04	13
34754	0.5	06039800900265	03 411	_17_	10 121_	65	_04_	_13
34755	07	08028001020258	05 504	18	12 142	53	04	09
34821	09	10066002410765	04 633	22	18 162	53	04	11
34822	80	07049001920528	04 571	23	12 122	59	04	11
34823	09	08067702020719	05 707	15	14 130	_55_	_05_	_11
34824	06	03003500210044	05 700	33	15 152	60	05	11
34825	80	09063902020574	07 565	18	11 127	58	05	10
34841	09	07052601810582	05 561	21	15 141	57	04	10
34842	09	09063101500492	09 594	20	17 149	54	06	10
34843	10	08059001470615	09 497	20	14 135	56	04	14
34844	08_	07044101200368	04 551	20_	12 141	59	04_	09
34845	09	10077002200644	08 516	15	12 142	61	05	11
34851	11	10066803250548	09_437_	16_	14_121_	75	_04_	_10
34852	09	09033601910378	03 462	21	18 132	51	04	11
34853	11	03067201900629	08 652	20	14 137	57	04	10
34854	11	08040002240418	07 551	20	13 132	60	04	09
34855	11	_10078302500724_	09_467	21_	14 121_	_56_	_04_	12
34911	06	11063001850483	06 554	21	13 133	57	04	11
34912	09_	_12064503150583_	08 434	_10_	13 146_	49	_04_	_11
34913	12	09035502500528	09 539	24	12 133	59	04	13
34914	12	07075002750708	06 523	16	10 130	60_	04_	12
34915	09	09058502100533	08 561	32	12 133	56	04	10
34921	09	08047801760507	08 549	17	12 136	62	04	11
34922	07	08050501530590	10 525	16	10 121	57	04	14
34923 34924	<u>08</u> 09	<u> 06034000920358</u> 03054901820567	09 495	_ <u>1 ರ_</u>	11 123	5 7	04	12
34925	07		07 615	24	16 170	58	04	09
34931	13	06036000900247 12060203320595	05 444	23	13 150 14' 150	67	04	09
34932	11	10059502370750	10 544	34 31	18 170	60 55	05	10 12
34933	13	10072304000840	07 697	23	14 143	_ 6U	04	08
34934	13	11064503700898	09 606	19	15 155	60	04	13
34935	11	09085202680743	05 656	35	13 161	60	06	10
34941	10	10058902800544	09 574	19	10 136	64	04	12
34942	09	07042001200315	07 564	18	10 133		04	10
34943	10	10052102500916	00 586	20	13 130	59	04	11
34944	11	13060002550749	03 498	17	08 126	65	04	15
34945	0.8	09053501920685	09 542	_18_	13 125	55 	04	12
34951	13	08060303220794	08 566	$\frac{13}{27}$	12 121	<u> 55</u>	05	10
34952	05	07032101000299	07 531	17	10 142	50	06	11
34 753	05	06040000760226	04 492	20	12 123	61	05	08
34954	07	_07041501310389	04 525	21	14 140	53	05	11
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35011	18	10063303540943	06 603	22	13 135	60	04	13

1	2	3 4	5 6	7	8 9	10	11	12
35012	07	07046301370403	08 559	19	17 155	56	04	11
35013	11	05055001400474	10 395	19	11 135	55	04	80
35014	20	07072503150888	10 541	19	14 152	53	07	10
35015	11	08069602500589	10 618	19	12 145	59	05	09
35021	12	07047202300895	08 558	24	11 129	54	04	12
35022	10	06040401980423	09 461	19	11 137	61	07	80
35023	09	07037101840569	03 625	21	15 144	56	04	11
35024	10	08059302560738	05 648	26	10 139	61	05	10
35025	22	10103406351566	08 567	19	12 140	58	05	09
35031	09	07055001200437	05 504	18	14 138	53	06	08
35032	10	08041501950554	08 570	24	14 121	54	08	10
35033	09	06032001260397	10 512	20	10 121	60	04	09
35034	08	10058502350622	05 600	21	11 139	53	04	11
35035	14	11068003941228	10 564	22	15 161	67	05	12
35041	11	07042901190595	10 501	20	12 140	46	04	12
35042	11	10053803140700	07 574	23	12 140	51	06	11
35043	13	08065802350676	06 635	22	13 132	53	04	10
35044	17	08060104450793	06 583	18	15 143	55	04	08
35045	17	12072305211463	08 689	15	15 155	52	05	13
35051	13	12107303700710	06 590	21	13 122	49	04	10
35052	80	07047401120307	10 571	16	12 144	60	04	11
35053	12	11076005051065	06 633	20	16 161	53	04	08
35054	05	03010000170073	02 706	28	14 135	61	06	11
35055	09	06091301200551	09 538	19	12 115	51	06	09
35311	80	05026701740357	01 384	15	10 115	56	04	09
35312	11	06018000980236	02 523	28	11 115	45	04	09
35313	14	08050003240723	02 466	16	12 120	5 ხ	04	11
35314	23	071460034)0833	10 519	20	15 164	64	04	15
3 53 15	09	08034301550530	02 450	16	13 115	57	05	10
35321	13	07046403470540	06 532	19	10 124	64	04	11
35322	08	07037801200254	03 382	16	13 126	63	04	14
35323	06	_06025500660205_	_05 492	17	09 118	63	04	13
35324.	10	10046102350490	02 465	lσ	12 131	73	04	12
35325	10	10036002420471	09 327	20	17 142	63	04_	15
35331	16	09062003820439	04 406	17	13 120	61	05	13
35332	09_	06019300900229	04 453	2 i	15 129	61	05	11
35333	10	07059802900400	03 671	36	13 147	59	06	13
35334	13_	08055201030453	00 557	29	10 115	59	04	09
35335	09	05043303270844	00 568	30	18 123	53	04	12
35341	0.8	10037501670311	04 503	20	11 131	59	04	13
35342	06	07030400750258	05 458	18	14 153	60	05	10
35343	10_	10050001820511	05_509_	26	_12_156_	60	04	14
35344	12	09031402620456	05 497	23	14 150	64	04	14
35345	09	_08060001570394	03 482	22	14 134	63	06	11
35351	11	11055503220687	03 506	3 I	12 110	46	04	14
35352	09	09046401570309	02 408	28	10 112	63	04	11
35353	13	07060602050330	00 492	28	11 115	56 47	04	10
3535 <u>4</u> 35355	12	09044202630484	04 538 06 371	18	13_134_ 16_162	61	04	13
32323	10	08029901640360	00 311	16	10 102	11	UT	13
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KEY TO APPENDIX TABLE 3

Column no.	<u> Item</u>
1	Row plot identification. The first digit indicates group number; the second and third, stand number; the fourth, mother tree number; and the fifth, replicate number.
2,3,4	Data not pertinent to the study.
5	Number of seeds sown.
6	Number of seeds germinated as of 3/29.
7	Number of seeds germinated as of $4/10$. Col. 7 x 100 = germinability in per cent. Also, Col. 5 Col. 6 x 100 = speed of germination in per cent. Col. 7
8	Sum of the numbers of cotyledons on a sample of seedlings (see Col. 9).
9	Number of seedlings on which cotyledon counts were made. Col. 8 = number of cotyledons per seedling. Col. 9
10, 11	Data not pertinent to the study.

Appendix Table 3.--Progeny data of Nursery Test 2

		2	2	,	r	4	7	ø	0	10	7.7
	1	2	3	4	5	6	7	8	9	10	11
	10111	399	56	10	44	38	41	74	10	39905600014035	9268
	10112	338	57	10	44	39	42	70	10	33805700016864	9286
_	10113	412	61	10	42	36	38	73	10	41206100014806	9474
	10121	346	44	10	44	13	18	67	10	34604400012717	7222
	10122	323	35	10	44	14	24	64	10	32303500010836	5833
	10123	271	43	3.0	42	09	12	63	10	33885375015867	7500
	10131	306	<u>42</u> 39	10	44	20	31 29	71		30604200013725	6452
	10132 10133	301 281	39 39	10	44	03 16	31	66 67	10	30103900012957 28103900013879	
	10141	403	49	10	44	17	24	70	10	40304900013579	5161 7083
	10142	356	44	10	44	11	24	67	10	35604400012139	4583
	10143	429	51	10	44	$\frac{13}{13}$	20	65	10	42905100011888	6500
	10151	375	48	10	44	26	33	74	10	37504800012800	7879
	10152	405	55	10	44	19	32	71	10	40505500013580	5938 -
	10153	445	50	10	43	22	34	67	10	44505000011236	6471
	10211	353	45	10	44	18	23	76	10	35304500012748	7826
	10212	321	47	10	44	1.7	-25	75	10	32104700014642	6800
	10213	383	58	10	44	11	15	76	10	38305800015144	7333
	10221	420	47	10	44	25	32	66	10	42004700011190	7813
	10222	405	49	10	44	26	31	68	10	40504900012099	8387
	10223	365	45	10	44	19	20	66	10	36504500012329	6552
	10231	388	41	10	44	24	31	69	10	38804100010567	7742
	10232	413	45_	10	44	_28_	35	_72_	10	41304500010896	8000
	10233	416	52	10	43	19	32	70	10	41605200012500	5938
	10241	333	35	10	44	09	23	66	10	33303500010511	3913
	10242	330	35	10	44	14	27	64	10	33003500010606	5185
	10243	377	44_	10	44	18	31	64	10	37704400011671	5806
	10251	359	39	10	44	13	21	69	10	35903900010864	6190
	10252	482	52_	10_	44	30	34	72	10	48205200010788	8824
	10253 10311	443	47	10	44	17 25	30 36	70 73	10	44304700010609	5667 6944
	10312	370	56	10	44	24	33	72	10	411041000 J976 37005600015135	7273
	10313	327	44	10	43	30	34	68	10	32704400013456	8824
	10321	291	36	08	44	01	04	25	04	36384500012371	2500
	10322	354	44	10	44	05	08	54		35404400012429	6250
	10323	389	48	10	43	07	12	71	lu	38904800012339	5833
	10331	441	53	10	44	23	25	72		44105300012018	9200
	10332	38L	63	10	44	21	24	75		38106300010535	8750
	10333	410	54	10	43	19	21	75	10	41005400013171	9048
	10341	424	63	10	44	23	29	68	10	42406300014858	7931
	10342	363	54	10	44	29	31	70	10	36305400014876	9355
	10343	407	55	10	44	24	30	68	10	40705500013514	8000
	10351	430	56	10	44	07	13	7੪		43005600013023	5385
	10352	383	58	10	44	20	30	79		38305800015144	6667
	10353	368	49	10	44	10	18	_78_		36804900013315	5556
	10411	401	46	10	44	13	19	76		40104600011471	6842
	10412	394	50	10	44	_22_	33	76	10	39405000012690	6667

1	2_	3	4	5	6	7	8	9	10 11	
10413	362	41	10	44	26	31	77	10	36204700012983 8387	
. 10421	332_	55	10	44	14	25_	79_	_10	33205500016566 5600	
10422	381	49	10	44	21	26	82	10	38104900012861 8077	
10423	344	54	10	44	27	31	79_	10	34405400015698 8710	
10431	391	5 8	10	44	17	20	76	10	39105800014834 8500	
10432	338	43	10	44	26	_28_	74_	_10	33804300012722_9286	
10433	337	53	10	44	20	25.	77	10	33705300015727 8000	
10441	321_	51	10	44	20	37	64	_10	32705700017431 5405	
10442	272	44	10	44	33	33	66	10	2720440001517610000	
10443	30ਰ	62	10	44	23	27	67	10	30806200020130 8519	
10451	060	09	02	44	01	01	14	02	3000450001500010000	
10452	122	17_	04	44	03	06	_34	05	30504250013934 5000	
10453	107	14	04	43	02	04	20	03	26753500013084 5000	
10511	333_	46	_10_	44	_17_	28	79_	_ 10	33304600013814_6071	
10512	383	52	10	44	8.0	2.7	76	10	38305200013577 2963	
10513	355	45	09	43	04	11	74	10	39445000012676 3636	
10521	364	58	10	44	32	32	80	10	3640580001593410000	
10522	383	56_	10	_44_	24_	_26_	71_		38305600014621 9231	-
10523	400	64	10	44	18 15	23 25	74	10	40006400016000 6429 34704300012392 5769	
10531 10532	<u>347</u> 362	43	_10 10	44	07	27	68 64	10	36204400012155 2593	
10533	364	50	10	44	05	17	64	10	36405000013736 2632	
10541	354	44	10	44	14	22	72	10	35904400012256 6364	
10542	331	50	10	44	20	30	68	10	33105000015106 6667	
10543	304	45	09	43	07	08	59	09	33785000014803 8750	
10551	338	40	10	44	22	23	_71	10	33804000011834 9565	
10552	388	45	10	44	21	23	77	10	38804500011598 9130	-
10553	387	64	10	44	12	20	76	10	38706400016537 6000	
10611	429	46	10	44	13	38	73	LU	42904600010723 3421	
10612	369	50	10	44	11	31	73	10	36905000013550 3548	
10613	391	64	10	43	30	26	68	10	39106400016368 3077	
10622	364	43	10	44	10	12	70	16	36404300011813 8333	
10623	308	61	09	44	01	0ฮ	59	0 હે	34226777819805 1250	
10621	385	51	10	44	80	11	65	04	38505100013247 7273	
10631	161	36	05	44	03	07	39	05	32207200022360 4286	
10632	441_	60_	_10_	44	_ 15	16	79_	_10	44106000013605 9375	
10633	341	49	09	43	06	11	72	09	37895444414370 5455	
10641	348_	65	10	44	11	25	70	_10	_34806500018678_4400	
10642	327	42	10	44	18	28	68	10	32704200012844 6429	
10643	403	63	10	44	06	22	70		40306300015633 2727	
10651	380	63	10	44	25	28	77		38006300016579 8929	
10652	366_	61	10	44	23_	24_	_74_		36606100016667_9583	
10653	352	52	10	42	07	17	69		35205200014773 4118	
10711	363	59	10_	44_	21_	24	71_		36305900016253_8750	
10712 10713	396	54 57	10	44	16	23	72	10	39605400013636 6957	
10713	<u>395</u> 400	57 49	10	44	<u>05</u> 13	1 i	72		39605700014394 4545	-
10721	381	44	10	44	08	23 16	72 75		40004900012250 5652 38104400011549 5000	
10723	311	40	10	44	05_	12	77		31104000012562 4167	
10731	396	53	10	44	30	28	78		3960530001338410714	
				77		20			2700220001230410114	

1_	_2_	_3	4_	_5_	6	7	8	9	10	_11_
10732	406	54	10	44	28	34	79	10	40605400013300	8235
10733	417	52	10	44	23_	31_	74	10	41705200012470	7419
10741	361	64	10	44	35	36	69	10	36106400017729	9722
10742	331	52	10	44	31	38	69	10	33105200015710	8158
10743	343	54	10	44	22	30	70	10	34305400015743	7333
10751	502	62	_10	44_	32	34	70	10	50206200012351	the second secon
10752	386	57	10	44	25	31	66	10	38605700014767	8065
10753	411	56	10	44	27	34	65	10		7941
10811	449	59	10	44	24	27	83	10	44905900013140	8889
10812	393	50	10	44	23	25	79	10	39305000012723	9200
10813	451	61	10	44	20	23	78	10	45106100013525	8696
10821	412	45	10_	44	05	07	_58_	07	41204500010922	7143
10822	452	51	10	44	10	13	83	10	45205100011283	7692
10823	125	50	03	44	03	03	16_	02	416756667136001	
10831	431		10	41	28	29	89	10	43105000011601	
10832	413	<u>46</u> 57	10	<u>40</u> 33	36 28	36 28	84	10	413046000111381	
10833 10841	377	55	10	44	23	35	80	10	37705500014589	
10842	428	50	10	44	38	38	_80_ 82	10	428050000116821	
10843	419	59	10	44	33	35	79	10	419059000110321	
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15443	_362	52	10	44	09	17	80	10	36205200014365 5294

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23013	477	71	10	44	13	19	85	10	47707100014835	
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24111	332	44	10	44	28	31	74	10	33204400013253	
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24143	305	44	10	44	06	15	63	10	30504400014426	
24151	308	49	10	44	14	31	76	10	30804900015909	The second secon
24152	314	42	10	44	08	29	72	10	31404200013376	

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34943	081	50	10	43	29	34	62	IU	8105000061728 8529
34951	161	38	10	44	24	37	66		16103800023602 6486
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35321	134	65	10	31	12	11	62	10	13406500048507	0000	
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BIOGRAPHICAL SKETCH

Anthony E. Squillace was born September 16, 1915, at Kinney, Minnesota. In June, 1933, he was graduated from Martin Hughes High School. After 3 years of temporary employment with the Civilian Conservation Corps and U.S. Forest Service, he resumed schooling at the Virginia Junior College, and University of Minnesota, earning a Bachelor of Science degree in Forestry from the latter in 1940. From 1940 to 1942 he was employed by the Consolidated Water Power and Paper Company at Grand Marais, Minnesota. From 1943 to 1945 he served with the U.S. Army in the United States and Europe. In 1946 he began permanent employment with the U.S. Forest Service, serving as Research Forester at stations in Montana, Washington, and Florida, and, aside from interruptions for further schooling, has continued in this position to the present time. He obtained a Master of Science degree in Forestry and Botany at the University of Montana in 1955, and enrolled in the Graduate School of the University of Florida in 1960.

Anthony E. Squillace is married to the former Dorothy Alice Babbini and is the father of three children. He is a member of the Society of American Foresters, Xi Sigma Pi, Phi Sigma, and Gamma Sigma Delta.

This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Agriculture and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

April 18, 1964

M. A. Brooker

Dean, College of Agriculture

L. E. Grinter Dean, Graduate School

Supervisory Committee:

A. T. Wallace, Chairman

W. O. Ash

Cloudlonger A. D. Confer

& Harde

R. E. Goddard

C. M. Kaufman

G. R. Noggle

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